Flow-related threats to rare galaxiids in the upper Waitaki River

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Contents

Abstract

Human activities are increasingly altering ecosystems, and are especially severe in streams where flow modification can affect environments far downstream and can interact with other pressures, such as species invasions. This has led to a disproportionately high number of threatened species in streams (e.g., native galaxiid fishes in New Zealand). I investigated how threatened bignose galaxias (*Galaxias macronasus*) and upland longjaw galaxias (*Galaxias prognathus*) were affected by flow-related influences in their habitats. A survey of sub-catchments in the Mackenzie Basin showed that flow regulation played a strong role in influencing fish occurrence; native fishes dominated unregulated rivers and introduced species dominated regulated rivers. Upland longjaw galaxias (ULG) were sparsely distributed and only found in unmodified braided rivers. Targeted surveys in these rivers indicated their habitat selection was weak, and although habitat availability was high, individual habitats were only occupied for short periods because floods frequently reconfigured the river bed. Thus, disturbances played a major role in ULG populations, forcing a strategy of weak habitat selection and frequent movement. This also makes them vulnerable to large-scale flow changes making the habitat more benign and potentially increasing competition (e.g., from invasive trout). Bignose galaxias were only locally abundant in very low discharge habitats lacking other fishes, so were restricted to very small parts of the river network. An experiment manipulating flows showed bignose galaxias moved into slower habitats over the short-term, suggesting a slow-flow preference, but not excluding the competitive influences of other fish like trout. Overall, this work shows these threatened fishes are susceptible to many of the current and future global changes affecting freshwaters like habitat alteration and invaders, but the above knowledge should allow targeted management of these influences for these highly threatened endemic fish.

Frontispiece. Upstream view of Fork Stream. Bignose galaxias (*Galaxias macronasus*) are common in springs which originate on the floodplains of braided rivers such as those in the lower left of the photograph.

Chapter One:

General Introduction

Global changes

Disturbances are agents of change which occur naturally in ecosystems, and shape the distributions of resources and organisms both spatially and temporally (Resh *et al.* 1988, Townsend, Scarsbrook and Doledec 1997, Ward 1998). Organisms occurring in these naturally disturbed ecosystems evolve adaptations which minimise the negative effects of the disturbances. (Southwood 1977). Consequently, these organisms are typically adapted to 'fit' their current environments (Southwood 1977, Lytle and Poff 2004). However, human activities are increasingly imposing changes to ecosystems, creating novel disturbances and altering existing ones, disrupting ecosystem processes, and changing the environments which organisms encounter (Vitousek *et al.* 1997, Chapin *et al.* 2000). The rate and scope of these changes is linked to increasing human populations and development. Therefore, following patterns in human population growth, the majority of these changes have been recent, rapid and global in extent (Vitousek *et al.* 1997, Chapin *et al.* 2000). These changes skew the 'fit' of organisms to their environment, causing changes to their distribution and populations. In this thesis I investigated how populations of threatened fishes, bignose galaxias (*Galaxias macronasus*) and upland longjaw galaxias (*Galaxias prognathus*), currently respond to changes in their habitats to inform how alterations due to global changes are likely to affect their populations in the future.

Global changes and freshwater ecosystems

Global changes to freshwater ecosystems have been summarised as resulting from: flow modification, habitat degradation and destruction, species invasions, over exploitation and water pollution (Dudgeon *et al.* 2006). Specific features which characterise freshwater ecosystems make them especially susceptible to global changes, particularly climate changes. For example, freshwater ecosystems are constrained, well defined systems leading to small geographic range and high endemism in freshwater species (Dudgeon *et al.* 2006, Strayer and Dudgeon 2010). These characteristics may make species in freshwater environments especially vulnerable to global changes because they cannot easily move to alternative habitats when local conditions change (Thuiller, Lavorel and Araujo 2005). Moreover, biodiversity in freshwaters is contained in a relatively small area, (0.8 % of the Earth's surface), concentrating biodiversity in freshwaters (Dudgeon *et al.* 2006).

Stream ecosystems are also particularly vulnerable to global changes due to the linear, unidirectional and dendritic arrangement of flowing freshwater ecosystems (Frissell *et al.* 1986). These characteristics link processes acting across scales in stream ecosystems, meaning upstream and downstream processes are linked, and processes act according to hierarchy of scales, from catchment-scales down to microhabitats (Frissell *et al.* 1986, Wiens 2002). Therefore, changes which affect processes at large scales, flow through stream networks and modify processes at smaller scales, combining the effects of changes over multiple scales. For example, catchment-scale changes in land use can increase fine sediment transport into streams, sediments are carried downstream at a rate determined by discharge, where they settle dependent on small-scale hydraulic features such as eddies and local velocity conditions (Sutherland, Meyer and Gardiner 2002). This means changes in local habitats may be the result of changes to multiple processes acting across differing, and often

interacting, scales making freshwater ecosystems vulnerable to the multiple and often interacting drivers of global change.

Finally, stream ecosystems may be especially vulnerable because they are strongly influenced by a powerful driver, the flow regime, which is linked to catchment-scale conditions, topography, climate and the connectivity of stream channels (Poff *et al.* 1997). In turn, flow regimes have large influences on ecosystem function, species interactions and disturbances (Meffe 1984, Resh *et al.* 1988, Biggs, Nikora and Snelder 2005), which in turn influence community composition and diversity (Death and Winterbourn 1995, Ward 1998, Kennard *et al.* 2007). Therefore, global changes may be especially damaging in stream ecosystems because multiple global change drivers (i.e. climate, land-use and in-stream habitat changes) are likely to interact to alter the flow regimes (Rosenberg, McCully and Pringle 2000), reducing diversity (Poff and Zimmerman 2010).

Consequently, the high biodiversity, hierarchical arrangement and the large influence of flow regimes, makes freshwater ecosystems especially vulnerable to global changes. Furthermore, these drivers, in close association with impacted terrestrial systems and human populations, have led to greater declines in biodiversity in freshwaters than in other systems (Sala *et al.* 2000). The consequences of global changes are likely to be especially severe for rare or threatened species. Contemporary populations of species which are threatened have usually already undergone large declines in their populations and distribution, in most cases this reflects the historic effects of the global changes described above (Strayer and Dudgeon 2010). Moreover, threatened species may be particularly vulnerable to altered habitat suitability because their reduced populations and distributions likely limit the ability of their populations to shift habitats (Hulme 2005, Thuiller, Lavorel and Araujo 2005). Therefore, understanding the effects of both past and future global changes on threatened freshwater

species is important for predicting how changes to freshwater environments should affect threatened species in order to manage changes to their environment.

Threatened galaxiids

New Zealand galaxiids have been affected by many of the global changes described above resulting in reductions to their populations, and consequently half of all described New Zealand galaxiids are considered threatened and the majority of the remaining half are at risk (Goodman *et al.* 2014). Specifically, threats to galaxiids include changes to their habitat, invasions of introduced fishes and modification of flows (Crowl, Townsend and McIntosh 1992, McIntosh *et al.* 2010).

In this thesis I investigated how two species of threatened galaxiid fishes (family: Galaxiidae), upland longjaw galaxias (*Galaxias prognathus*) and bignose galaxias (*G. macronasus*), responded to current changes and patterns in their environment, in order to better understand how mechanisms which drive their populations will respond to future global changes. Both species occur in the upper Waitaki River, a single large catchment in New Zealand's South Island which has undergone: extensive dam development for generation of hydro-electricity, continued land use modification and irrigation development for agriculture, and supports fisheries of introduced salmonids for recreation and aquaculture. Bignose galaxias are endemic to the upper Waitaki River catchment and are largely restricted to small streams which flow from springs and wetlands throughout the region. Upland longjaw galaxias are native to the region and are found in large braided rivers which drain catchments to the east of New Zealand's Southern Alps. Both fishes I studied are likely to have undergone reductions in their populations and distribution due to flow modification, habitat degradation and species invasions. However, any changes are largely undocumented because the species are either rare (upland longjaw galaxias; Chapter Three) or recently

discovered (bignose galaxias; Chapter Four). Therefore, investigation of the mechanisms which currently influence these threatened fishes is needed to determine the likely outcomes of future global change.

Thesis Organisation

I have organised the thesis into three data chapters which are written as stand-alone manuscripts (Chapters Two – Four) to be later submitted for publication, and a final chapter (Chapter Five) which integrates and further discusses findings from the three data chapters. Figures and tables are included at the end of chapters and their numbering begins for each.

In Chapter Two, I used a nested survey design to investigate the influence of habitat variables from different scales on the distribution of fishes in the upper Waitaki River and how these habitat variables from different scales interact. The survey contrasted regulated and unregulated rivers and main stem and spring-fed flow sources, as well as meso- and micro-habitat variables. I further used aggregated species abundances to investigate differences in fish community structure between regulated and unregulated rivers.

I determined during surveys described in Chapter Two that populations of upland longjaw galaxias were only found in main stems of large braided rivers characterised by large and frequent flow disturbances. Therefore, in Chapter Three I investigated the response of upland longjaw galaxias populations to these disturbances using temporal surveys. I used a novel survey approach to further assess their distribution within main stem braided riverbed habitats to determine patterns in the availability and use of habitat in relation to microhabitat variables across the riverbeds. Furthermore, because species able to withstand disturbances may also be susceptible to competitive interactions, I also surveyed other fish populations to determine any competitive effects on upland longjaw galaxias.

In Chapter Four, I investigated, using temporal surveys across a disturbance gradient, how populations of bignose galaxias (*Galaxias macronasus*), a spring-fed habitat specialist galaxiid, were affected by naturally changing flows. In spring-fed streams bignose galaxias co-occured with native and introduced competitors, so I also investigated the role of changing flows on these competitors, and the influence of competitors on bignose galaxias. Based on the patterns found in the temporal survey, I then used an in-stream flow manipulation experiment to test the short-term effects of changes in flows on bignose galaxias.

In Chapter Five, the final chapter, I draw together the results of each data chapter in relation to how populations of these fishes might respond to future changes in their habitat. I further integrate these results into a framework which highlights the multiple global changes that threatened fish populations face. I conclude by using specific management examples for each species to illustrate how conservation of these fishes should view their populations within a much wider framework that incorporates multiple global changes and characteristics of stream ecosystems.

Plate 1. Photographs of stable spring-fed streams (upper) and disturbed and braided rivers (lower) typical of those in the upper Waitaki River.

Chapter Two:

Multi-scale influences, including flow regulation, on fish populations and communities in a New Zealand River.

Introduction

Biological communities are typically regulated by a combination of biotic and abiotic controls (Jackson, Peres-Neto and Olden 2001) and in stream ecosystems, these controls are often hierarchically organized (Frissell *et al.* 1986) and scale-dependent (Levin 1992, Cooper *et al.* 1998, Jackson, Peres-Neto and Olden 2001). For example, disturbances can act across a variety of spatial scales, while biotic controls such as predation and competition, tend to act at smaller scales (Jackson, Peres-Neto and Olden 2001, Mims and Olden 2012). Understanding the ecological processes structuring fish communities and implementing effective management will therefore likely require knowledge of the scale at which these ecological processes operate to influence local populations and communities (Cooper *et al.* 1998). Identifying the relative importance of variables from multiple scales will especially help identify which processes are likely to be the most important for rare and threatened fish species and the influence of invaders on native fish populations. The hierarchical and dendritic nature of stream ecosystems means that when changes are made to larger scale processes then the effects of those changes are likely to influence smaller scales (Richards, Johnson and Host 1996, Allan 2004, Brazner *et al.* 2005). Thus, changes at smaller scales are likely to have more localised effects, while changes at larger scales are likely to have extensive impacts on processes at subsequent within nested spatial scales (Allan 2004). Furthermore, physical processes acting at multiple scales may interact to influence

ecosystems processes, although studies testing the effects of interacting scales in freshwaters are rare (Poizat and Pont 1996, Kennard *et al.* 2007). In this study I investigated the influence of multiple and interacting habitat variables on the presence of rare fish species at different scales within a catchment exhibiting diverse (both natural and artificial), flow regimes.

In freshwaters, the major driver of habitat conditions at large scales is the flow regime; the quantity, variability and predictability of stream discharge (Poff *et al.* 1997). Prevailing flow regimes drive key geomorphic processes that form and maintain habitat conditions in stream ecosystems (Poff *et al.* 1997) and are often a product of wider-scale climatic and geographic conditions which interact at subsequent scales to affect the shape and nature of channels (Petts and Gurnell 2005, Elosegi, Diez and Mutz 2010). Thus, flow regime influences on stream faunas may occur via changes to multiple habitat variables acting across multiple spatial and temporal scales. Since stream faunas may respond differently to different components of the flow regime, the effects of flow regimes on resident fauna will be highly scale-dependent. Thus, understanding how flow regimes affect stream habitats across those scales will likely be critical for predicting how human alterations to stream discharges affect stream faunas.

Defining spatial scales most relevant to the organism in question is important, and Frissel et al. (1986) introduces five successively smaller 'habitat subscales' which provide a useful classification (Townsend and Hildrew 1994), ranging from the largest spatial scale of the entire stream system (1000's of metres), down to microhabitat (0.1 m) scales. Under this classification, for example, the characteristics of the pool/riffle subsystem will be determined by subsequent reach-scale (10's of metres) subsystems. The pool/riffle scale in Frissell et al. (1986), is consistent with mesohabitat (Boys and Thoms 2006), macrohabitat (Maddock

1999) or physical biotope (Newson and Newson 2000) classifications elsewhere and will be referred to herein as ‘mesohabitat’.

Arguably, the most influential driver of change in flow regimes is flow regulation (Nilsson *et al.* 2005). Flow regulation is a pervasive human-induced disturbance in freshwater ecosystems, common in both developed and developing countries (Nilsson *et al.* 2005, Poff *et al.* 2007), that alters the timing and magnitude river flows(Magilligan and Nislow 2005). These changes associated with flow regulation can influence the processes that drive habitat conditions in rivers, causing changes in downstream river characteristics such as sediment fluxes (Petts and Gurnell 2005), channel dimensions and sinuosity, and influencing riparian vegetation (Brandt 2000). Thus, because flow regulation influences a wide range of habitat conditions, and can affect large areas of river habitats, the impacts of flow regulation on fish communities can be severe and widespread (Poff and Zimmerman 2010, Carlisle, Wolock and Meador 2011).

Changes to flow magnitudes generally have negative impacts on fish communities and diversity (Poff and Zimmerman 2010), with communities in regulated rivers often being different to those in unregulated rivers, and frequently dominated by non-native species (Pringle, Freeman and Freeman 2000, Marchetti and Moyle 2001, Bunn and Arthington 2002). In New Zealand fish communities observed above and below dams differ, with exotic species dominating above-dam fish communities (Jellyman and Harding 2012). Most indigenous New Zealand freshwater fish are from the family Galaxiidae (i.e. galaxiids), with the majority (68 %) of galaxiids, particularly non-migratory species, considered threatened or in decline (Allibone *et al.* 2010). Habitat modification and interactions with introduced salmonids are the major factors associated with these declines and threats (McDowall 2006). Furthermore, many non-migratory galaxiid species have been described only relatively

recently (McDowall and Waters 2002, McDowall and Waters 2003), and have highly restricted distributions when compared to other native migratory species. Therefore, non-migratory galaxiid populations are especially susceptible to changes in flow regimes, either directly through habitat condition modification or indirectly, due to negative interactions with non-native fishes, which predominate in regulated rivers. Therefore, knowledge of how changes to flow regimes influence the availability of habitats for native fish will be crucial for understanding their ecology and managing their conservation.

This aim of this study was to determine how flow-related habitat variables affected fish populations and communities in a New Zealand catchment (the Waitaki River) with substantial flow regulation. The Waitaki River catchment was chosen because it is home to several threatened galaxiid species, including lowland longjaw galaxias (*Galaxias cobitinis*), upland longjaw galaxias (*G. prognathus*) and bignose galaxias (*G. macronasus*) occur there (Allibone *et al.* 2010), and strong contrasts in flow regime exist between the regulated and unregulated streams in the catchment (Figure 1). The specific aims of this study were to determine: 1) the relative influence of habitat variables with different scales on fish communities and individual species, 2) how habitat variables from different scales interact and, 3) how native and non-native fishes differ in their responses to flow regulation, across the multiple scales investigated.

Methods

Site description

The Mackenzie Basin, is a large glacially-formed basin east of the Southern Alps, South Island, New Zealand (Figure 2A). The entire basin forms the upper catchment of the Waitaki River and has undergone extensive hydroelectric development utilising both natural and artificial lakes as storage reservoirs. Consequently, riverbeds downstream of these storage

lakes have changed substantially (Mosley 1982) and currently receive predominantly stable flows with low fluctuations in discharge and a lack of high discharges. In contrast, unregulated rivers in the catchment receive aseasonal high and low flows common to New Zealand disturbed alpine rivers (Winterbourn, Rounick and Cowie 1981). Sampling sites were selected to include both regulated and unregulated rivers in the basin (Figure 2A). The study focused on sub-catchments where threatened galaxiid species had been previously found. Existing distribution information and habitat descriptions (McDowall and Waters 2003) were used to select sub-catchments where threatened galaxiid species were known to occur.

Survey design

This study was concerned with how habitat variables from multiple scales affect fish distributions, so a hierarchical survey approach was used, incorporating four spatial scales and associated habitat variables (Table 1). Habitat variables were selected to represent contrasts in environmental conditions at multiple scales and because multiple variables were measured at each site, consideration was given to the ease of measurement for each variable. At the largest scale, one kilometre square sub-catchments were selected and classified as regulated or non-regulated based on the presence of upstream dams, and were selected to represent broad differences in flow regime. Within sub-catchments, stream segments were classified based on the source of flow into either spring-fed or main stem segments to represent natural contrasts in local flow conditions. Spring-fed segments were identified as fed by springheads, or upwelling zones in braided rivers which were located and traced to their sources during on foot field surveys. Main stem segments included the main stem of the largest channel in a sub-catchment and its tributaries. Within the sub-catchment stream segments, the mesohabitat type of sampling reaches was classified as either, pool, riffle, or

run, based on an assessment of surface flow type and channel dimensions at the reaches. Eight mesohabitat types (riffle, pool, run, glide, cascade, rapid, bedrock outcrop, marginal deadwater and macrophytes) were, initially used in the survey, as described by Newson and Newson (2000), based on a visual assessments of surface flows and bed profile. Not all mesohabitat types were represented in all sub-catchments, so the types used were aggregated for analysis. Ponded mesohabitat types were not considered, so were removed from analysis. Rapid mesohabitat types were combined with the riffle mesohabitat type to represent mesohabitats with high velocities, while pool mesohabitat types were combined with glide mesohabitats to represent low-velocity mesohabitats. The composition of mesohabitats and source of flow segments was expressed using percentage area composition of each mesohabitat type. During sampling mesohabitat types and source of flow were mapped as segments of stream and types recorded for each segment. Segment lengths were combined with widths collected at each sampling location to estimate the total area of each mesohabitat and segment type across the entire area sampled. Total area of each mesohabitat type was used to calculate a percentage area for each mesohabitat in each sub-catchment to standardise mesohabitat composition across streams of differing sizes. Differences in percentage area of mesohabitat types between regulated and non-regulated sub-catchments, and main stem and spring-fed sources of flow, were tested using a multivariate analysis of variance (MANOVA) on arcsine square-root transformed percentage areas. Differences in the composition of sources of flow between regulated and unregulated sub-catchments were tested using analysis of variance on arcsine square-root transformed percentage areas.

Timing and logistic restraints meant that velocity was not measured at sampling locations, however, sampling was undertaken at Fraser Stream to test for the ability of the classifications of mesohabitats to distinguish between hydraulic conditions, and especially whether velocity differed between mesohabitat types. Velocity measurements were taken

after fish sampling in Fraser Stream to avoid any bias in mesohabitat assignment and were tested among mesohabitat types using ANOVA.

At the smallest scale, microhabitat variables were measured at each sampling location within mesohabitats, and included wetted width, depth and a coded visual estimate of substrate coarseness. Substrate coarseness was estimated using a visual assessment of percentage cover of substrate classes based on the Wentworth scale where each substrate class was assigned a weight according to particle size (Harding *et al.* 2009). The percentage cover of each class was then multiplied by a substrate class weighting and the product was summed across each substrate class and divided by 100 to give a final score between seven and one. High scores represented a dominance of coarser substrates, similar to the score used in Jowett and Richardson (2008), although with weightings taken from a modified Brusven Substrate Index (Harding *et al.* 2009). The effectiveness of this visual estimate was tested against a sample of particle sizes taken from sub-sampling locations in Fraser Stream. Thirty particles were sampled at sub-sampling locations using the methods described in Wolman (1954) and particles were measured along their b-axes. The relationship between visual estimates of substrate coarseness and the median particle sizes from samples was assessed using a Pearson's correlation coefficient.

Fish Sampling

Fish-sampling locations were selected from within the one km^2 area in each sub-catchment (Figure 2A) so that source-of-flow, segment types and mesohabitats were sampled in proportion to their abundance in sub-catchments based on ground-mapping of catchments. Previous distributions of fish species were determined using records from the New Zealand Freshwater Fish Database (NZFFD, managed by the National Institute of Water and Atmospheric Research) and one km^2 within each sub-catchment was chosen to lie within the

known distributions of both bignose galaxias and upland longjaw galaxias. Starting from the main stem of each sub-catchment, stream segment lengths were mapped on foot using a handheld global positioning system (Recon XC, Trimble Navigation). During mapping, all wetted channels in the one km^2 area were identified and source-of-flow, and mesohabitat types were recorded (Figure 2C, 1D). While mapping, sampling locations were assigned based on distances between locations drawn from random values between 25 m and 75 m, meaning between 45 to 60 locations were sampled in each sub-catchment. Locations were sampled in an upstream direction to prevent the influence of downstream fish movement following fishing. Where locations were unable to be sampled, typically because high depth or velocity prevented safe fishing, the closest location suitable for fishing was sampled. A backpack operated electofisher (Kainga EFM 300, NIWA Instrument Systems, Christchurch, New Zealand), typically operated at 600 V due to low conductivity, was used to sample sites and the same operator was used throughout. At each sampling location, three downstream passes of two-metres length were made with an electrofishing machine into a 0.9 m wide pole seine (i.e. approximately 1.8 m^2 was sampled per pass) which was spread across the width of the immediate channel. In addition, habitat variables were measured across the channel at each location. Captured fish were removed from the stream, identified and their total natural lengths measured to the nearest mm. Fish were then released after completion of sampling at each site.

Statistical analysis

My survey sampled nested levels of habitat variables to evaluate the relative influence of each spatial scale of habitat on the presence of fish species. Several species were absent from at least one of the sub-catchments surveyed so survey data was limited to include only sub-catchments where previous records showed that the species had been previously found or

where the species was found during surveys. A two-stage analysis approach was used to first compare candidate models and then a final reduced model was determined using parameters from high-ranking models in the candidate set. This was done by firstly testing competing models using an information-theoretic approach (Burnham and Anderson 2002). Secondly, reduced models were determined by sequentially removing variables until further removal of variables no longer improved model fits using AICc. Parameters that were included in the candidate models with evidence ratios of less than ten were used to produce a starting model before model reduction. Competing binomial generalized linear mixed models (Bolker *et al.* 2009) based on species presence/absence with habitat variables from either single or multiple spatial scales, and including potential interactions between scales, were also assessed using an information-theoretic approach (Burnham and Anderson 2002). Channel width, depth and substrate coarseness were grouped as microhabitat variables and all were included in a candidate model which included microhabitat spatial scale. All combinations of spatial scales were included in candidate model sets up to two-way interactions, including combinations of scales up to a model where all spatial scales were included. Models with all possible two-way interactions were also included for candidate models with more than one spatial scale. Microhabitat variables were continuous and were $\log_n$-transformed to reduce the influence of large values. Candidate models were fitted using a mixed modelling approach with the 'lme4' package (version 1.0-5) in R Program (R Core Team 2014) to allow for the hierarchically arranged data (Zuur *et al.* 2009a). Each candidate model contained the same nested error terms to reflect the nested structure of the survey and included random intercepts for each sub-catchment sampled. The binomial response (with a logit link), presence of fish caught at each sampling point was used because the original response, number of fish caught per sample, was strongly over-dispersed. Canterbury galaxias (*G. vulgaris*) and koaro (*G. brevipinnis*) were grouped for analysis because they were difficult to reliably differentiate in

the field using morphological characters (McDowall and Hewitt 2004) and are hereafter referred to as koaro. The coefficients of determination, conditional and marginal r-squared (Nakagawa and Schielzeth 2013), were calculated along with evidence ratios for reporting of model selection results.

To evaluate and visualise differences in fish community composition between sub-catchments, I used a non-metric multidimensional scaling (NMDS) ordination based on species abundances using a Curtis-Bray dissimilarity index in the *vegan* package (2.0-9) in R program (R Core Team 2014). Abundance was expressed as catch per unit effort (CPUE), and calculated using the total number of captures of the species at the sub-catchment and the corresponding effort (pushnet passes, see above). CPUE was used because the effort applied across streams varied between one and five 'pushes' into a stop net. The number of pushes was therefore used as a measure of capture effort. Lowland longjaw galaxias, upland longjaw galaxias and bignose galaxias were removed from the community structure analysis because their distributions were restricted, and they occurred in less than half of the sub-catchments surveyed. Differences in community composition between regulated and unregulated sub-catchments were tested using a permuted ANOVA (PERMNOVA; Anderson 2001) to evaluate, for each catchment separately, the hypothesis that samples were from either, regulated or unregulated sub-catchments. A multivariate homogeneity of groups dispersion (PERMDISP; Anderson 2006) test was used to determine significant differences in group dispersions between fish communities in regulated and unregulated streams.

Results

The proportion of main-stem or spring-fed segments did not significantly differ between regulated and unregulated sub-catchments (ANOVA; $F_{(1,7)} = 5.43$, $P = 0.052$) with unregulated sub-catchments having only slightly larger proportions of spring-fed segments

(Figure 3A). Similarly, the composition of mesohabitat types did not differ between regulated and unregulated sub-catchments (MANOVA; $F_{(3,5)} = 0.46$, $P > 0.7$; Figure 3B). However, the mesohabitat composition of main stem segments differed significantly from the composition of spring-fed segments within both regulated and unregulated sub-catchments (MANOVA; $F_{R/F\,(6,12)} = 10.0832$, $P < 0.001$). Spring-fed segments had higher proportions of pool habitats in both regulated and unregulated sub-catchments and lower proportions of run and riffle mesohabitats (Figure 3C). Visual measures of mesohabitat and substrate coarseness represented respective differences in stream velocity and median substrate particle size. Current velocities differed significantly between mesohabitat types ($F_{2,47} = 20.51$; $P < 0.001$); mean velocity was highest in riffle habitats, run habitats had intermediate velocities, and pool habitats had low velocities according to pairwise Tukey post-hoc comparisons. Substrate coarseness score was positively correlated with the median particle size of the calibration samples (Pearson's correlation coefficient: $R = 0.78$, $t_{(1,33)} = 7.3$, $P < 0.001$).

Covering the four scales (Table 1) a total of 404 locations from nine sub-catchments were sampled between April and July 2010 with, 49, on average, per sub-catchment. Overall 1078 fish were captured with native fish species accounting for 84 % of captures across all surveyed sub-catchments. However, in regulated sub-catchments native fish comprised only 60 % of captures, whereas in unregulated sub-catchments they comprised 94 % of captures. Koaro were the most abundant species being found in all sub-catchments and having the highest catch per unit effort (Table 2). The second most abundant species was upland bullies, followed by alpine galaxias. Both longjaw galaxias species (lowland longjaw galaxias and upland longjaw galaxias) were found in low abundances and were present in a low percentage of samples, even in sub-catchments where they are known to have occurred. Brown trout and rainbow trout CPUE was lower than for galaxiid species, however they were present in a comparable proportion of samples as other species, reflecting their low numbers of fish per

sample but relatively high occurrence. Several species were absent from one or more of the sub-catchments surveys. Lowland and upland longjaw galaxias were both found during this survey but their low abundance and restricted distributions prevented further quantitative analysis for these species using this sampling design. Lowland galaxias were captured in Fraser Stream, where only five individuals were caught (Table 2). Although they have been recorded in both Edwards Stream and the lower Ohau River previously (NZFFD), they were not found in these sub-catchments during surveys. Upland longjaw galaxias were captured only in the Cass and Godley Rivers, although their known distribution placed them in sampled areas in both the Ahuriri and Tasman Rivers. Bignose galaxias were only found in the Ahuriri River and Fraser Stream sub-catchments (Figure 2A). Their recorded distribution includes Edwards Stream and the lower Ohau River (NZFFD), and locations of recorded presences in Edwards Stream were within sampling areas, so sampling locations from Edwards Stream were included in the analysis. Records from lower Ohau River, however were restricted to a single location 3 km upstream of the sampling area, despite records for other species throughout the sub-catchment, so the lower Ohau River was not considered in analyses for bignose galaxias. Alpine galaxias were found in four sub-catchments during surveys; the Ahuriri River, Cass River, Edwards Stream and Godley River. They were not captured in Fraser Stream or Tekapo River in this survey, however previous records (NZFFD) from within the sampling area meant these sub-catchments were included for analysis. The statistical effects of flow regulation were unable to be evaluated for bignose galaxias and alpine galaxias because these species were not found in any regulated sub-catchments during surveys. Similarly, alpine galaxias were mostly absent from pool mesohabitats in the study so these mesohabitats were excluded from analysis. Tasman River sampling locations were removed from the analysis for rainbow trout, and Edwards Stream locations for brown trout, because there were no records of their presence in these sub-

catchments, despite extensive records throughout these sub-catchments. Koaro, and upland bullies, were captured in all sub-catchments included in this survey and so were subject to analysis using the full set of sub-catchments.

Performance of presence-absence models varied between species (Table 3). For alpine galaxias, model selection showed a clear best model which included source of flow and microhabitat variables channel width, depth and substrate compactness as well as interactions between channel depth and width and source of flow. Best models for koaro and brown trout included flow regulation, source of flow and mesohabitat type. In both cases, the best models were over four times more likely than the next best model to based on AICc and had marginal R^2 values of over 0.25 meaning 25 % of the variation in the data was explained by these models. The best model for upland bullies included flow regulation, mesohabitat and microhabitat, and a closely competing model also included source of flow. Competing models for rainbow trout were more closely tied. The top ranking candidate model was 1.2 times more likely to represent the best trade-off between model complexity and explanatory power than the next best candidate model. The three top-ranked models all included flow regulation (Table 3). The second and third ranked models also included, mesohabitat and source of flow, respectively and the second ranked model included an interaction between flow regulation and mesohabitat (Table 3).

Habitat variables from multiple scales were included in top-ranked models for five out of six of the species found in the survey. Furthermore, habitat variables from each of the spatial scales (Table 3) were represented at least once in models that best explained the occurrence of a species. Thus, multi-scale influences were important in explaining the presence of fish populations in this study. The sub-catchment-level variable, flow regulation, was included in the best models for all species for which it was included in the candidate set of models (Table

3). Flow regulation was particularly influential on brown and rainbow trout occurrence. It was included in the best models for both species (Table 3) and the occurrence of both species was highest in regulated sub-catchments (Figure 4A, Figure 4B). Among native fish, models best explaining occurrences of koaro and upland bullies also included effects of flow regulation (Table 3). The occurrence of upland bullies was highest in regulated catchments and was also dependent on the mesohabitat type, with the probability of their occurrence being highest in pool mesohabitats (Figure 4C). Koaro occurrence was generally higher in unregulated catchments but this depended on interactions between flow regulation and mesohabitat type. In regulated sub-catchments they were predominantly present in riffle meso-habitats, while in unregulated catchments their presence was generally higher and less dependent on mesohabitat (Figure 4D).

Source of flow was particularly important for galaxiid species and was included in the best models for all galaxiids (Table 3). The presence of koaro depended on source of flow via an interaction with mesohabitat type, whereby their occurrence was highest in riffle mesohabitats in spring-fed segments (Figure 4D) while mesohabitat was relatively unimportant in main stem segments. Alpine galaxias presence was best explained by source of flow via an interaction with channel width (Table 3) whereby the probability of their presence was highest in wide channels and the shape of this relationship differed between main stem and spring-fed segments (Figure 5A). Their occurrence also increased with channel depth in main stem segments, but declined with increasing depth in spring-fed segments (Figure 5B). Bignose galaxias presence was best explained by a model with source of flow only (Table 3) because their occurrence was highest in spring-fed segments and they were seldom present in main stem segments (Figure 6A). Source of flow was also included in the best model explaining brown trout occurrence (Table 3) where their probability of

occurrence was highest in spring-fed reaches, in regulated and unregulated sub-catchments (Figure 4B).

Mesohabitat type was included in the highest-ranked candidate model for koaro, upland bullies and brown trout (Table 3). Upland bully occurrence was highest in pool mesohabitats and lowest in the fast-flowing run and riffle mesohabitat types (Figure 4C) regardless of both flow regulation and source of flow. The probability of brown trout presence also differed between mesohabitat types. Their presence was highest in the fast-flowing riffle habitats and lowest in slower-flowing pool meso-habitats (Figure 4B). There were no interactions between mesohabitat type and any other habitat variables, so the effect of meso-habitat type on brown trout occurrence was independent of both flow regulation and source of flow.

Microhabitat conditions were included in the models best explaining alpine galaxias, upland bully and rainbow trout presence (Table 3). The probability of alpine galaxias presence increased with substrate coarseness (Figure 5C). Whereas, channel width was included in the best model explaining rainbow trout occurrence (Table 3) where their occurrence decreased with channel width (Figure 6B). Channel depth was included in the best model explaining upland bully occurrence, the probability of their presence declined with increasing channel depth. Catchment-scale flow regulation had a particularly large influence on the presence of the species surveyed and was included in the best models for all species where it was able to be tested, and was important for both native and introduced species. Interactions between habitat variables from differing scales were included in the best models for two out of the six species tested.

Fish communities were significantly different between regulated and unregulated sub-catchments (PERMANOVA; $F_{(1,7)} = 3.32$, $P = 0.023$), with NMDS ordination showing clear separation of fish communities between regulated and non-regulated catchment types (Figure

7). Group dispersion was not significantly different between communities in regulated and unregulated catchments (PERMDISP; $F_{(1,7)} = 1.85$, $P = 0.22$). These patterns were mainly driven by communities with high abundances of brown trout, rainbow trout and upland bullies in regulated sub-catchments (Figure 7).

Discussion

Ecological processes operate across a wide range of spatial scales and typically act in concert to produce observed ecological patterns (Levin 1992). The role of spatial scale in stream ecosystems is well-recognised (Cooper *et al.* 1998, Esselman and Allan 2010) and studies incorporating multiple scales are common (Joy and Death 2004, Leathwick *et al.* 2005, Esselman and Allan 2010), however the role of interactions between spatial scales is not well understood.

The aim of this study was to determine how habitat variables across multiple spatial scales influenced fish communities and species occurrences, and how these responses differed between native and non-native species. While the occurrence of individual fish species were influenced by habitat variables from multiple spatial scales, fish communities were influenced by flow regulation while community structure was not tested at other scales. Community differences in regulated sub-catchments were driven by the high abundance of the two salmonid species, brown trout and rainbow trout, and upland bully. In comparison, unregulated sub-catchments had higher abundance of koaro and an absence of alpine and bignose galaxias. The influence of flow regulation was also apparent in the models of individual species occurrences and was included in models for all the species for which it could be tested.

The effect of flow regulation on species occurrences followed community patterns with trout species and upland bullies having higher occurrence in regulated sub-catchments and

galaxiids having lower occurrence in unregulated sub-catchments. The reduced occurrence of trout in unregulated streams was unlikely to be related to a lack of access because salmonids were encountered in all of the sub-catchments sampled, and sources of salmonid colonists were present in reservoirs downstream of unregulated sub-catchments. Therefore, the strong community differences between regulated and unregulated streams very likely reflect flow-related factors acting on these communities. The predictability and variability of flow regimes shape community structure with alterations to natural flows affecting the structure of fish communities (Bain, Finn and Booke 1988). Additionally, alterations to flow regime can increase the likelihood of establishment of non-native species (Moyle and Light 1996, Pringle, Freeman and Freeman 2000, Marchetti and Moyle 2001, Bunn and Arthington 2002), and changes in hydrology towards more stable flow conditions often favour non-native species which can displace native species which are frequently better adapted to more natural flows (Bunn and Arthington 2002). Therefore, the lower incidence of hydrological disturbances and the alteration of the flow regime in regulated sub-catchments may have facilitated the high levels of trout presence in regulated sub-catchments. Once established, trout would be expected to have a competitive advantage over native species in both behavioural and predatory interactions (McIntosh 2000, McDowall 2006) and are shown to locally extirpate native galaxiids species where they become established (Crowl, Townsend and McIntosh 1992, McIntosh *et al.* 2010).

Source of flow was particularly influential in explaining the occurrence of native galaxiid species. For example, the higher occurrence of bignose galaxias in spring-fed streams follows previous descriptions of their presence being associated with perched wetlands or spring-fed streams (McDowall and Waters 2003). Source of flow was also included, along with other habitat variables as interaction terms, in models of koaro and alpine galaxias abundance. The occurrence of koaro in riffle mesohabitats was higher in spring-fed segments. Brown trout

occurrence was also higher in spring-fed segments over main stems. However, unlike for the galaxiid species, source of flow did not interact with other habitat variables. In this study source of flow can be considered a surrogate for flow variability. Spring-fed segments were typically lateral to the main stems of sampled rivers and would not be expected to experience the same range of high and low flows. This is likely to benefit fish which are less able to withstand high flows such as bignose galaxias which are seldom found in the main stems of rivers and are not known to possess any obvious morphological features that would enable them to withstand high flows. However, I found both brown trout and koaro were more often present in spring-fed segments rather than in main stems. Koaro are especially adept at withstanding high flows (Jowett and Richardson 2008), and their increased presence in spring-fed segments is unexpected. Possible explanations are that spring-fed segments provide a refugia from disturbances which affect the main stems, which are even utilized by species able to withstand high flows.

Mesohabitat was included in the best models for koaro, upland bully and brown trout. Koaro and brown trout favoured higher velocity riffle mesohabitats while upland bullies preferred slower pool habitats. These patterns are consistent with known velocity preferences for these species; faster velocities for koaro and brown trout and slower velocities for upland bullies (Jowett and Richardson 2008). Similarly the absence of mesohabitat may reflect a lack of velocity preference or preference for intermediate velocities in both rainbow trout and alpine galaxias (Jowett and Richardson 2008). Microhabitat variables explained the occurrences of alpine galaxias, upland bully and rainbow trout. Alpine galaxias occurrence increased with increasing substrate coarseness and decreased with depth and rainbow trout occurrence was highest in coarse substrates. These patterns match previous descriptions of their habitats and preferences (McDowall 2006, Jowett and Richardson 2008).

My study design allowed me to test the effect of interactions between habitat variables from differing spatial scales. In addition to the influence of the habitat variables discussed above, interactions were found in models explaining koaro or Canterbury galaxias and alpine galaxias occurrence. Such interactions suggest that the influence of habitat variables at more local scales are not independent of habitat variables at larger scales. For example, koaro were more often found in riffle mesohabitats, but this pattern was strongest in regulated sub-catchments. Likewise, alpine galaxias presence was influenced by microhabitat variables, but these relationships were dependent on the source of the flow in the surrounding stream segment. This has large implications for how information based on surveys of limited scale are generalized across catchments as patterns derived from more local scales may be a result of the larger scale catchment conditions.

The community patterns in this study may also be interpreted in a life-history framework. The sub-catchments in this study were selected to represent regulated and unregulated streams, providing a strong contrast in flow regime. I found strong differences in community composition between regulated and unregulated sub-catchments. Changes to flow regimes are known to affect the composition of fish communities (Bain, Finn and Booke 1988). Furthermore, the direction of these changes, and which species are likely to be favoured by, or be susceptible to changes to flow regimes, can be linked to their life history traits. Life history theory for fish communities predicts that species with opportunistic life history traits, small body size, numerous poorly surviving offspring and low parental investment, should predominate in streams with low predictability in flows (Mims and Olden 2012). The galaxiid species found in the study region are small bodied and show a low investment in parental care (Closs, Hicks and Jellyman 2013). Galaxiid species were more commonly found in unregulated streams with unpredictable flow regimes fitting the expectation that opportunistic species predominate in streams with unpredictable flows. Conversely, species abundant in

regulated streams included those species that displayed traits associated with more "equilibrium" strategists (Mims and Olden 2012), such as longer generation times, larger sizes and increased parental investment. Trout are generally longer lived and larger than the non-migratory galaxiid species that occurred in unregulated sub-catchments. Upland bullies, while not larger than the galaxiid species, are known to display parental investment, establishing territories and actively defending them (Hamilton 1998). Such equilibrium strategist traits are predicted to be favourable to those species under conditions of low environmental variation (Mims and Olden 2012). In regulated catchments the increased stability of flow regimes may favour traits found in trout and upland bullies and may explain their predominance in regulated catchments. The absence of several galaxiid species from regulated streams in this survey may be a result of changes in abiotic conditions under the altered flow regimes in these rivers (Brandt 2000). Given the known impact of introduced salmonids on galaxiids (Crowl, Townsend and McIntosh 1992, McIntosh 2000, McDowall 2006), the absence of galaxiids may also be related to biotic factors such as competition and predation. If the lower incidence of high flows in these rivers has produced conditions favourable for trout, then the abiotic conditions that favour trout may produce the biotic conditions which makes these rivers less favourable for galaxiids.

Overall, threatened galaxiid species in this study were rare across the sub-catchments sampled, particularly upland and lowland longjaw galaxias. The rarity of lowland longjaw galaxias is expected given their very narrow distributions within catchments. However, upland longjaw galaxias and bignose galaxias were absent from several sub-catchments where they were known to have previously occurred. This absence may be due poor detection probability owing both to the coarse-scale sampling design and the sparse and patchy distribution of these fishes. Consequently, absences of rare galaxiids from regulated catchments were treated as true absences, preventing further analyses of the impact of stream

regulation on those species. However, this should not preclude the possibility that historical distributions of these species may have included currently regulated streams. Several human impacts are likely to have impacted their distribution prior to their discovery and their current distributions may not reflect their distribution prior to human impacts (McDowall and Waters 2003). Given the recent discovery of some of the threatened galaxiid species knowledge of their prior distribution is non-existent. Both Tekapo River and the lower Ohau River have upstream populations of bignose galaxias and alpine galaxias. Both species also occur in the nearby unregulated Ahuriri River, at similar stream sizes and elevation as both of these regulated rivers. The impact of introduced salmonids and habitat changes on galaxiid fishes, especially non-migratory species, are well established (Crowl, Townsend and McIntosh 1992, McIntosh 2000, McDowall 2006). Prior to the damming of these rivers flow regimes would have been much more unpredictable and the character of the rivers were substantially more braided (Mosley 1982). Changes in flow regimes are known to impact native species as conditions move from those they are adapted to (Bain, Finn and Booke 1988). Therefore, if these species were previously present in the currently regulated rivers, then changes in flow regime combined with the ongoing impacts of elevated trout abundance are likely to have restricted distributions of threatened galaxiids in the Upper Waitaki River, long before their discovery.

Conclusions

This research indicates that the influence of interacting habitat variables from multiple scales is important in explaining the occurrence of fish species in the upper Waitaki River catchment. This has important implications for managing galaxiid fishes in this catchment and prioritising the habitat requirements for these fish may require an approach that considers both the scales of habitat variables influencing these populations and the possible interaction

of these variables across spatial scales. In most cases, species presence was best explained using variables from across multiple spatial scales with the effects of narrow spatial scales nested within effects of broader scales. Surveys limited in spatial scale may identify certain habitat variables as being important, however these may be less important than habitat variables from other scales. This may be particularly problematic where patterns derived at limited scales are applied across broader scales. Alternatively, where interactions of habitat variables between scales are less important then the application of one-size-fits-all management options across broader scales should be more successful. Overall, this study suggests that the habitat variables affecting fish populations are hierarchical and act across multiple scales. The habitat variables which were important for individual fish species operated at differing scales and for several species multiple and sometimes interacting factors influenced their populations.

Tables and Figures

Table 1. Nested hierarchy of habitat variables included in candidate models and their associated scales. Abbreviations used in candidate model tables are also shown.

Scale	Extent	Habitat variable	Abbreviation	Categories
Sub-catchment	1000 m	flow regulation	R	regulated
				non-regulated
Segment	100 m	source of flow	F	main stem
				spring-fed
Mesohabitat	10 m	mesohabitat	M	run
				riffle
				pool
Microhabitat	1 m	width	w	continuous
		depth	d	continuous
		substrate coarseness	s	continuous

Table 2. Capture and occurrence information for fish species sampled in a survey of nine sub-catchments of the upper Waitaki River catchment, South Island, New Zealand. Total is the catch from all captures for a given species from electrofishing. Percent total and CPUE total are the percent occurrence at all sites and catch per unit effort across the entire study, respectively. % occur and CPUE occur are the percent occurrence and CPUE calculated only from sub-catchments where the species were present or have been previously present.

Common name	Scientific name	Total	% total	% occur	CPUE total	CPUE occur
bignose galaxias	*Galaxias macronasus*	30	2.8	12.7	0.03	0.10
upland longjaw galaxias	*Galaxias prognathus*	14	1.3	5.3	0.01	0.03
lowland longjaw galaxias	*Galaxias cobitinis*	5	0.5	2.7	0.00	0.02
koaro or Canterbury galaxias	*Galaxias brevipinnis or Galaxias vulgaris*	437	40.5	31.9	0.38	0.38
alpine galaxias	*Galaxias paucispondylus*	206	19.1	22.2	0.18	0.27
upland bully	*Gobiomorphus breviceps*	218	20.2	20.5	0.19	0.19
brown trout *	*Salmo trutta*	119	11.0	17.9	0.10	0.12
rainbow trout *	*Oncorhynchus mykiss*	49	4.5	9.8	0.04	0.05
native		910	84.4	62.4	0.80	0.80
salmonids		168	15.6	21.5	0.15	0.15
galaxiids		692	64.2	46.8	0.61	0.61

* denotes non-native species

Table 3. Model selection results for evaluating the influence of multi-scale habitat variables on species occurrence in a survey of nine sub-catchments of the upper Waitaki River catchment, South Island, New Zealand. Model terms specify the habitat variable being tested for given models (see Table 1 for abbreviations). Two-way interactions are shown as an asterisk separating habitat variables. Included terms are indicated with a filled circle and excluded terms are indicated with a dash. *K* is the number of parameters in the model, including terms for random effects and any interactions; *n* is the number of sub-sampling locations included in the model; AIC_c is Akaikes Information Criterion (with small sample size correction); Δ_i is the difference between the AIC_c of the given model and the model with the lowest AIC_c; ω_i is the Akaike weight and R^2m and R^2c are marginal and conditional r-squared values following Nakagawa and Schielzeth (2013). Evidence ratios were calculated using Akaike weights comparing subsequent models to the top model. Competing models are ordered according to the relative evidence for each and candidate models with evidence ratios greater than ten are omitted. Best models, were selected by either the next closest model having an evidence ratio higher than ten, or selected during model reduction, are shown in bold.

	Model terms																										
Species	R	F	M	w	d	s	R*F	R*M	F*M	R*w	R*d	R*s	F*w	F*d	F*s	M*w	M*d	M*s	K	n	AIC_c	R^2m	R^2c	Δ_i	ω_i	eRatio
koaro or Canterbury galaxias	•	•	•				•	•	•										11	404	419.1	0.28	0.41	0.00	0.80	1.0
		•	•						•										7	404	423.9	0.10	0.33	4.80	0.07	10.8
	•	•	•																6	404	425.3	0.17	0.32	6.20	0.04	21.9
	•		•					•											7	404	426.0	0.24	0.38	6.80	0.03	30.1
		•	•																5	404	426.2	0.08	0.31	7.10	0.02	34.9
	•	•	•					•	•										**10**	**404**	**417.2**	**0.27**	**0.41**	**-**	**-**	**-**
bignose galaxias	-	•					-	-		-	-	-							**3**	**126**	**70.2**	**0.45**	**0.55**	**0.00**	**0.59**	**1.0**
	-	•	•				-	-		-	-	-							5	126	72.5	0.47	0.57	2.30	0.19	3.1
	-	•		•	•	•	-	-		-	-	-							6	126	74.1	0.48	0.59	3.80	0.09	6.8
	-	•	•				-	-	•	-	-	-							7	126	74.1	0.95	0.96	3.90	0.09	6.9
alpine galaxias	-	•		•	•	•	-	-		-	-	-	•	•	•				9	199	156.1	0.39	0.81	0.00	0.83	1.0
	-	•		•	•	•	-	-		-	-	-							6	199	160.5	0.19	0.75	4.40	0.09	9.0
	-	•		•	•	•	-	-		-	-	-	•	•					**8**	**199**	**154.0**	**0.37**	**0.80**	**-**	**-**	**-**

	Model terms																								
Species	R	F	M	w	d	s	R*F	R*M	F*M	R*w	R*d	R*s	F*w	F*d	F*s	M*w	M*d	M*s	K	n	AIC_c	R^2m	R^2c	Δ_i	ω_i	eRatio
upland bully	•		•																5	404	337.9	0.28	0.36	0.00	0.48	1.0
	•	•	•																6	404	339.8	0.28	0.36	2.00	0.18	2.7
	•		•					•											7	404	340.4	0.30	0.37	2.50	0.14	3.5
	•		•	•	•	•													8	404	340.6	0.29	0.37	2.80	0.12	4.0
	•		•		•														**6**	**404**	**337.2**	**0.29**	**0.37**	**-**	**-**	**-**
rainbow trout	•																		3	356	223.1	0.09	0.09	0.00	0.29	1.0
	•		•					•											7	356	223.5	0.16	0.16	0.40	0.24	1.2
	•	•																	4	356	224.2	0.10	0.10	1.20	0.16	1.8
	•			•	•	•													6	356	225.8	0.12	0.12	2.70	0.07	4.0
	•	•					•												5	356	226.3	0.10	0.10	3.20	0.06	5.0
	•		•																5	356	226.8	0.10	0.10	3.70	0.04	6.4
	•	•		•	•	•													7	356	227.0	0.13	0.13	3.90	0.04	7.1
	•		•	•				•											**8**	**356**	**222.9**	**0.18**	**0.18**	**-**	**-**	**-**
brown trout	•	•	•																6	364	271.6	0.35	0.40	0.00	0.73	1.0
	•	•	•				•	•	•										11	364	275.7	0.37	0.43	4.10	0.10	7.7
	•	•	•					•											**8**	**364**	**270.3**	**0.34**	**0.39**	**-**	**-**	**-**

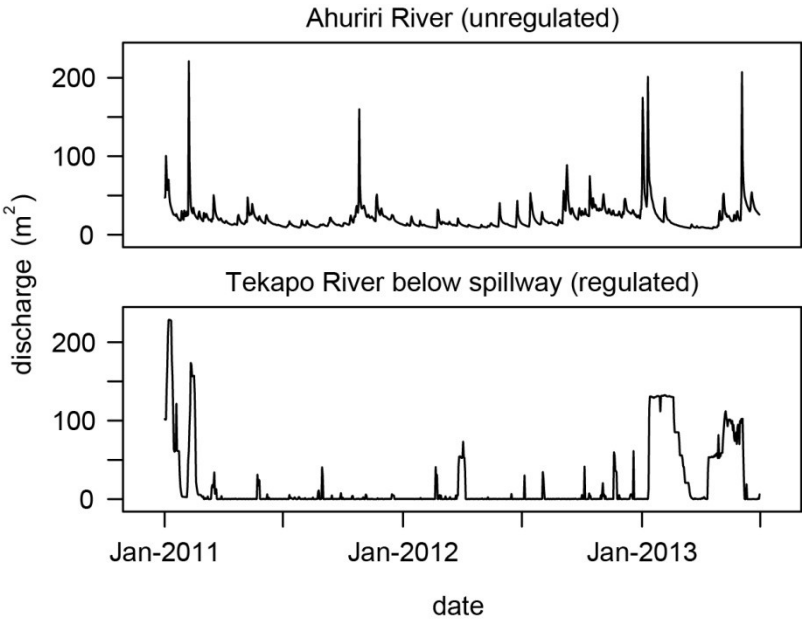

Figure 1. Typical hydrograph from the main stem of regulated and unregulated sub-catchments in the Upper Waitaki River. Daily discharge means for the study periods are shown.

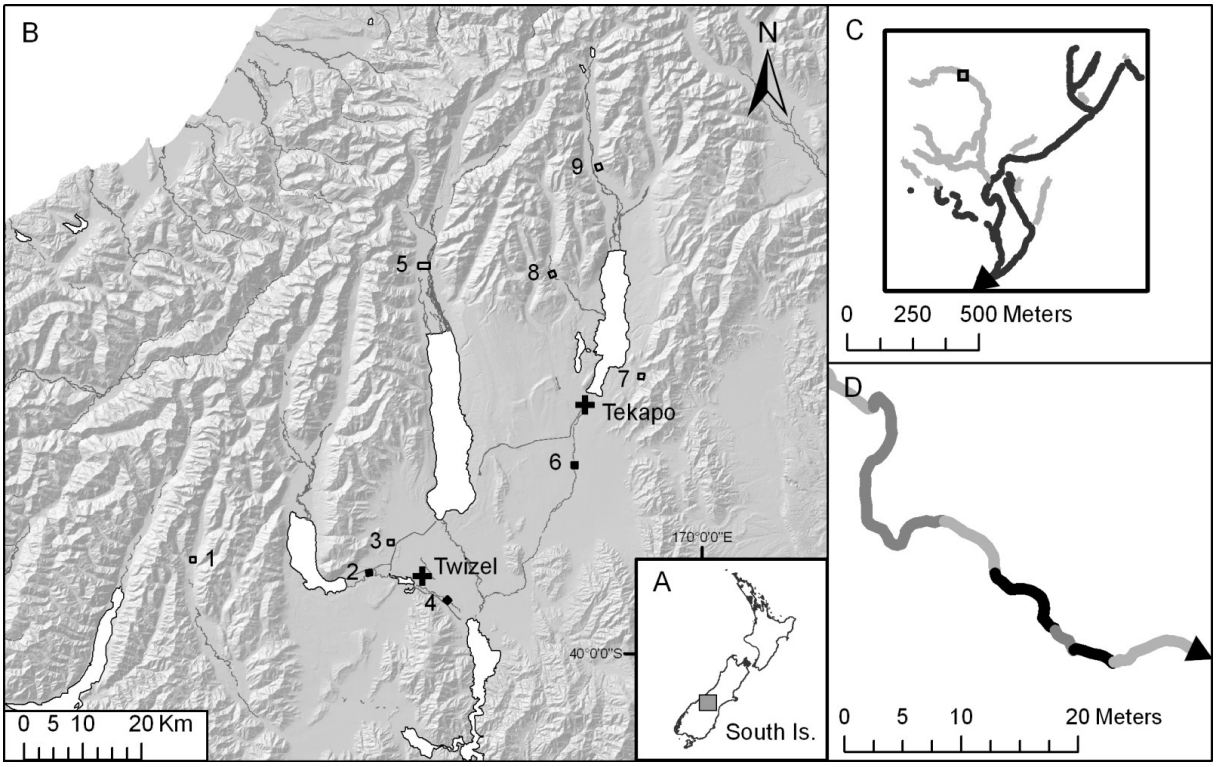

Figure 2. Distribution of sub-catchments in South Island New Zealand (A) in the upper Waitaki River (B) and examples of source-of-flow (C) and mesohabitat types (D) at segment and mesohabitat scales. (a) Locations of areas sampled in sub-catchments are indicated by squares with numbers corresponding to the following streams: (1) Ahuriri River, (2) Ohau River (upper), (3) Fraser Stream, (4) Ohau River (lower), (5) Tasman River, (6) Tekapo River, (7) Edwards Stream, (8) Cass River and (9) Godley River. Surrounding lakes and ocean are represented by white regions, and large rivers and canals are shown in dark grey. Source-of-flow segments are shown for Ahuriri River (C) indicating distribution of main stem (black) and spring-fed (grey) segments. (D) The distribution of mesohabitat reaches is shown for a spring-fed channel in the Ahuriri River. Riffle mesohabitat reaches are shown as black, run as dark grey and pool as light grey. Microhabitats within reaches (not shown) were the fourth spatial scale sampled.

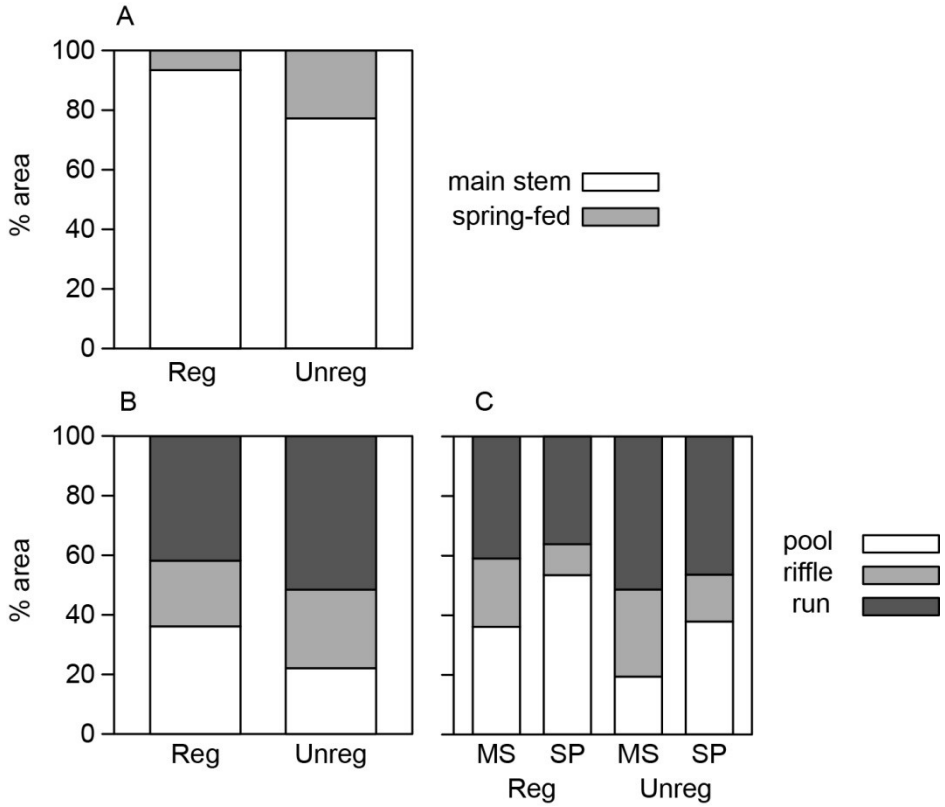

Figure 3. Percentage composition of mesohabitat types and source of flow segments in regulated and unregulated subcatchments. Bars represent the percentage composition of: (A) source of flow types across regulated and unregulated sub-catchments, (B) mesohabitat composition across regulated and unregulated sub-catchments (C) mesohabitat composition across source of flow within regulated and unregulated sub-catchments. Abbreviations for labels on the x-axis are Reg and Unreg correspond to regulated and unregulated sub-catchment types and MS and SP correspond to main stem and spring-fed sources of flow. Bar shading represents source of flow and mesohabitat and are shown in the legends to the right of figures.

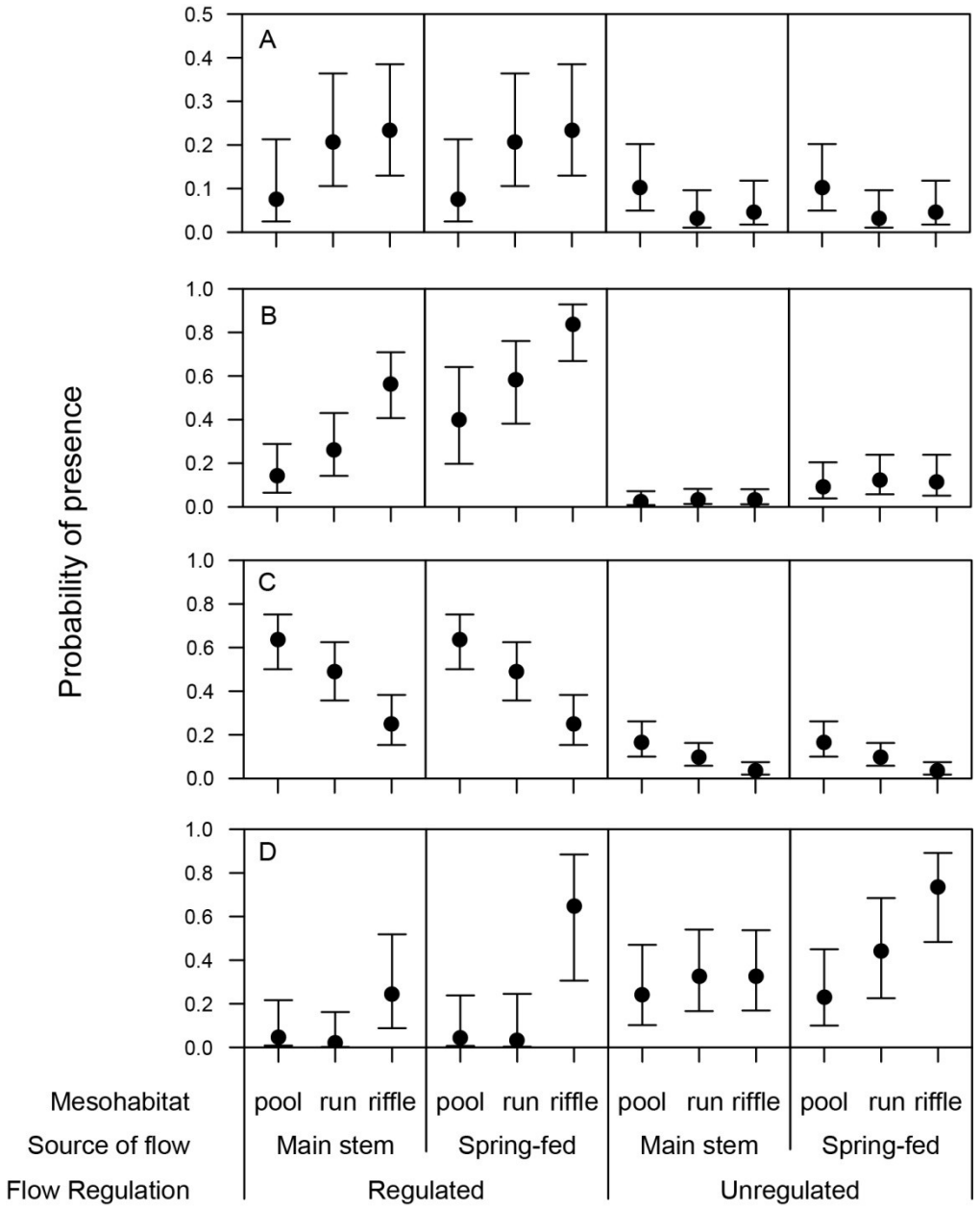

Figure 4. Fitted estimates of probability of presence of: (A) rainbow trout (*Oncorhynchys mykiss*); (B) brown trout (*Salmo trutta*); (C) upland bully (*Gobiomorphus breviceps*); and (D) combined koaro (*Galaxias brevipinnis*) and Canterbury galaxias (*Galaxias vulgaris*) based on top-ranked candidate models from a hierarchical survey of nine sub-catchments of the upper Waitaki River catchment, South Island, New Zealand in regulated and unregulated sub-catchments with spring-fed and main stem sources of flow and with nested mesohabitat types. Means are fitted values using model coefficients and error bars and bands and represent 95 % confidence intervals using the standard error of coefficients for fixed effects and horizontal axes represent nested multi-scale habitat variables.

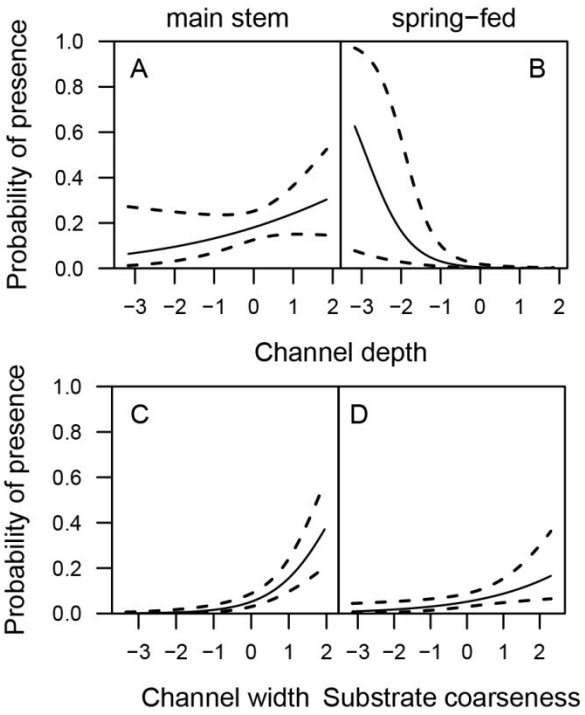

Figure 5. Fitted estimates for the probability of alpine galaxias (*Galaxias paucispondylus*) presence at sub-sampling locations based on top-ranked candidate models from a survey of nine sub-catchments of the upper Waitaki River catchment, South Island, New Zealand. The four graphs (A-D) depict the relationship between the probability of alpine galaxias presence and: channel depth in main stem (A) and spring-fed (B) stream segments; channel width (C) and substrate coarseness (D). Continuous variables were log-transformed, then mean adjusted and standardised, for analysis and standardized means are shown above. Means are shown as solid lines and represent fitted values using model coefficients. Error bars are shown as dashed lines and represent 95 % confidence intervals based on the standard error of coefficients for fixed effects.

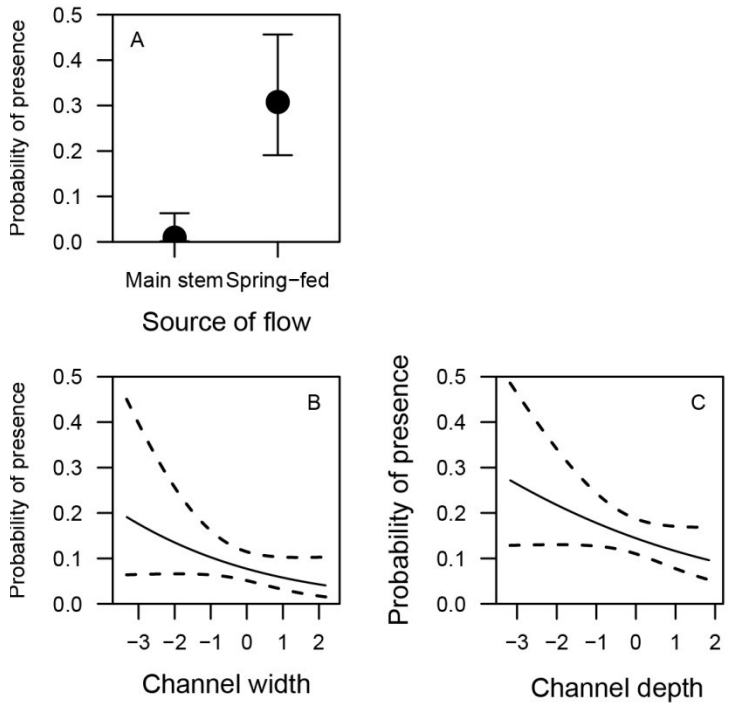

Figure 6. Probability of fish presence with source of flow and microhabitat variables based on top-ranked candidate models from a survey of nine sub-catchments of the upper Waitaki River catchment, South Island, New Zealand. (A) Probability of bignose galaxias presence in main stem and spring-fed stream segments. (B) Probability of rainbow trout presence with channel width and (C) probability of presence of upland bully with channel depth. Continuous variables were log-transformed, then mean adjusted and standardised, for analysis and standardized means are shown above. Means are fitted values using model coefficients and error bars and bands represent 95 % confidence intervals using the standard error of coefficients for fixed effects.

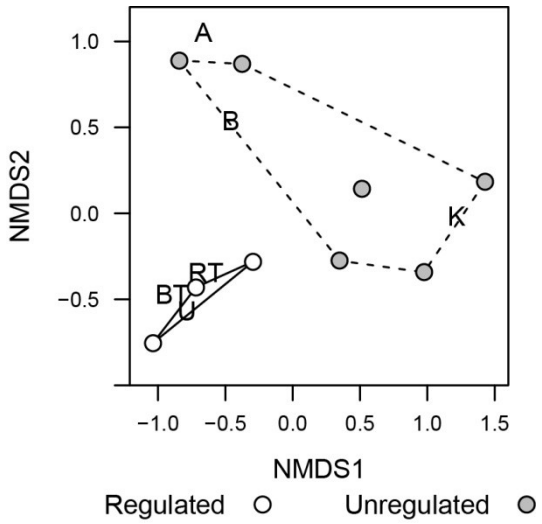

Figure 7. Ordination of fish communities in regulated and unregulated sub-catchments fitted using NMDS ordination. Open circles represent fish communities from regulated sub-catchments and gray circles represent unregulated sub-catchments of the Waitaki River. Convex hulls are drawn around groups, the solid line groups regulated, and the dashed line unregulated, sub-catchments. Species scores are shown as follows: (A) alpine galaxias (*Galaxias paucispondylus*); (B) bignose galaxias (*Galaxias macronasus*); (K) koaro (*Galaxias brevipinnis*) or Canterbury galaxias (*Galaxias vulgaris*); (RT) rainbow trout (*Oncorhynchus mykiss*); (BT) brown trout (*Salmo trutta*); (U) upland bully (*Gobiomorphus breviceps*). The stress value for the ordination is 0.046 and group centroids were significantly different (PERMANOVA; $F_{1,8} = 3.33$, $P < 0.025$).

Plate 2. Upland longjaw galaxias (*Galaxias prognathus*) are restricted to the upper catchments of large braided river valleys draining the eastern side of New Zealands' Southern Alps.

Chapter Three:

Habitat-use and abundance of upland longjaw galaxias (*Galaxias prognathus*) within highly-disturbed braided New Zealand rivers.

Introduction

Disturbances displace organisms and matter within ecosystems to varying magnitudes, frequencies and extents, making disturbed habitats especially challenging for populations to persist in (Resh *et al.* 1988). Organisms able to withstand disturbances, or re-colonise recently disturbed habitats, benefit from occupying habitats with reduced abundances of competitors (Townsend 1989, Jackson, Peres-Neto and Olden 2001). If disturbances are frequent and severe enough, densities of disturbance-prone competitors may even approach zero and disturbance-adapted species may experience little or no inter-specific competition (Southwood 1977, Townsend 1989). Species able to withstand disturbances, or re-colonise disturbed habitats, typically have broad habitat preferences and are able to occupy a wide range of habitats (Townsend, Doledec and Scarsbrook 1997). Traits, such as small size and investment in reproductive output instead or predatory defences, also enhance an organism's ability to persist in, or re-colonise, disturbed habitats (Southwood 1977, Townsend, Doledec and Scarsbrook 1997). The longevity and stability of habitats in disturbed environments is often low (van der Nat *et al.* 2003), so, by having generalist habitat preferences, organisms are able to persist for longer and in a wider range of habitats. However, traits that enable survival in disturbed habitats are also likely to make disturbance-adapted organisms especially susceptible to competitive interactions under more benign conditions (Townsend, Scarsbrook and Doledec 1997, Lytle and Poff 2004). Overall, species which benefit in disturbed environments should display traits which promote survival during disturbances, and

densities of their competitors should be reduced by disturbance. I examined the habitat use and population responses of a fish that occupies disturbed braided river environments. Habitat use was examined to determine whether they display generalist habitat use patterns which may promote persistence in disturbed environments and population responses were examined to determine how disturbances influence fish populations in these environments.

Among freshwater ecosystems, braided rivers are highly disturbed environments with dynamic and heterogeneous habitats characterised by large and frequent flows which mobilse their beds contributing to their physical character (Junk, Bayley and Sparks 1989, van der Nat *et al.* 2003, Malard *et al.* 2006). Flows continually reshape habitats within the floodplain by moving and removing substrates and organisms, and removing and establishing new channels (van der Nat *et al.* 2003). This maintains strong spatial and temporal gradients in local velocities, depths, substrate coarseness and temperatures, and, therefore, presents a wide variety of habitat types to organisms (Malard *et al.* 2006). Across braided river floodplains, these gradients support a variety of habitats which support diverse communities (Ward *et al.* 2002, Gray, Scarsbrook and Harding 2006). At the more disturbed end of these gradients, however, disturbances support low-diversity but stable communities as the community becomes limited to species with characteristics which enable them to withstand disturbances in these environments (Scarsbrook 2002). These characteristics include are short generation times, high mobility and weak habitat preferences (Townsend, Doledec and Scarsbrook 1997). Therefore, the composition of communities in braided rivers should comprise those species with characteristics which enable them to persist in these disturbed environments.

I investigated how disturbances affected the habitat-use of a threatened fish species, upland longjaw galaxias (*Galaxias prognathus*; ULG), which only occur in the catchments of large braided river catchments draining the eastern side of the Southern Alps, New Zealand

(McDowall 2006). ULG occur in braided main stems, tributaries and springs within catchments and typically occur at high elevations at the upper extent of catchments. Main stems of these catchments experience aseasonal high flows with large amounts of bed movement (Pearson and Henderson 2004). Furthermore, frequent disturbance limits productivity in these rivers, lowering algal, invertebrate and fish production (Death and Winterbourn 1995, Biggs *et al.* 2001, Jellyman, Booker and McIntosh 2013). ULG typically share habitat with alpine galaxias which has a much wider distribution and higher abundance within its range and is not considered threatened (Goodman *et al.* 2014). In considering if, and how, species like ULG persist, it is important to consider that the effects of disturbances are not uniform across species, and species often have characteristics which enable them to withstand (resistance) or recolonise (resilience) in disturbed habitats (Townsend, Doledec and Scarsbrook 1997). For fishes, physiological characteristics, such as streamlined body form, broad physiological tolerances and behavioural or life-histories which utilise non-disturbed habitats represent resistance traits (Townsend, Doledec and Scarsbrook 1997, Lytle and Poff 2004). Small body size, short generation times and high mobility may confer resilience to populations allowing rapid recovery following disturbances (Townsend, Doledec and Scarsbrook 1997). Knowledge of the traits which relate to ULG persistence in braided rivers are likely to be integral to their conservation.

An understanding of the factors which influence ULG populations is especially valuable because recent re-evaluation of ULG conservation status, ranks their current threatened status as 'nationally vulnerable' (Goodman *et al.* 2014) based on a moderately sized population of mature individuals and predicted future declines (see Townsend *et al.* 2008 for decline definitions). Their threatened status has steadily worsened over time from 'sparse' (Hitchmough 2002) to 'gradual decline' (Hitchmough, Bull and Cromarty 2007) and finally to 'nationally vulnerable' (Allibone *et al.* 2010, Goodman *et al.* 2014) and has retained a

'data poor' qualifier throughout. Because of their rarity, current understanding of the habitat requirements for this species is very limited. Jowett and Richardson (2008) summarised their habitat preferences based on national survey data which included only eight occurrences out of 154 locations sampled. Further information on this species is limited to only a few studies on their growth, size distribution, diet, and reproduction (Bonnett, Sagar and Docherty 1989, Bonnett 1990, Bonnett 1992), a study on the biogeography of longjaw galaxiids (Waters and Craw 2008) and general descriptions of their habitat (McDowall 2006) and distribution (Elkington and Charteris 2005). Significant knowledge gaps for ULG include a lack of information about their population dynamics, both temporally and spatially, and detailed descriptions of key habitats, for spawning and rearing, are also lacking. These gaps complicate studies of ULG by preventing targeted surveys of ULG in preferred habitats. For example, studies (Bonnett 1990) and records from the New Zealand Freshwater Fish Database show ULG also occur in springs adjacent to braided rivers in some, but not all, of the catchments in which they occur. However, my broad-scale surveys in Chapter One indicated ULG were sparse, were not found in regulated sub-catchments and were only found in main stems of rivers in the Upper Waitaki catchment during that survey. Therefore, my survey focused on determining habitat use patterns of ULG in the main stems of large braided river catchments. Currently, a lack of detailed knowledge of the habitat preferences of these fish may preclude any analysis of the impacts of changing river flows on their populations, therefore critically limiting efforts towards their conservation.

ULG possess many traits that suggest that their current life history could be adapted to disturbed environments; small size (Bonnett 1990), short generation times (Bonnett 1990), and a streamlined body form. In addition to these traits, species which are able to persist in disturbed environments are predicted under habitat templet theory (Southwood 1977) to have weak habitat preferences making them habitat generalists (Townsend and Hildrew 1994).

The specific aims of this study were to measure occurrence and abundance patterns for ULG across riverbeds, and to determine fates of populations at locations through time to evaluate the effects of flow disturbances on their populations. I also aimed to measure occurrence and abundance patterns of other fish species present to determine the effects of disturbance on overall fish abundance and community composition so that potential effects of other species could be evaluated. I predicted that fish abundance would decline following flow disturbances but that disturbance-related declines would be larger for fish species other than ULG. Additionally, I investigated whether ULG occurrence and abundance were related to the availability of micro-habitats associated with specific depth, velocity and substrate composition across riverbeds. I predicted that the influence of micro-habitat variables on ULG occurrence should be weak relative to other species, reflecting generalist habitat preferences which are likely to underpin and promote persistence of ULG in disturbed rivers. Overall, I expected that the influences of habitat variables on abundance would be weaker than those influencing occurrence, reflecting reduced overall competition for habitats because fish densities of both ULG and their competitors would most likely be low.

Methods

Study location

This study was carried out in three rivers located in the upper Waitaki River catchment known as the 'Mackenzie Basin' in the South Island of New Zealand. All the rivers originated in high altitude, glacially-fed catchments along the South Island's main divide and flowed east into large glacially-formed lakes which are regulated for the generation of hydro electricity. All rivers sampled had braided channels and had elevations above sea level of between 540 m and 880 m.

Sampling Design

Previous site visits and surveys in the Godley and Cass Rivers (see Chapter One; Figure 2) indicated that ULG were rare and sparsely distributed in the main stems of these braided rivers (Elkington and Charteris 2005). Given these low abundances and expected strong influences of flooding disturbance on ULG populations, a variety of sampling methods were used to determine the availability and use of habitats across the riverbed. Sampling was initially split into two types of samples, firstly from reaches known to contain ULG, hereafter called the 'selective sample', and secondly a random sample of the rest of the riverbed, called the 'random sample' (Figure 1). The basis of this split was that probabilistic sampling of the surrounding river would be most likely to yield information on variables influencing ULG occurrence, while sampling of reaches identified as already containing moderate abundances of ULG could yield information on variables influencing their abundance. Additionally, sites for a temporal comparison of fish populations, hereafter 'temporal sample', were established within selectively-sampled reaches (Figure 1).

During visits in December 2010, sites with moderate local ULG abundances, suitable for selective sampling, were identified using spot-fishing across all braided river reaches. When ULG were caught during spot-fishing from approximately five or more samples from the same reach, the reach was then identified as a possible selective-sampling site. High flows in December 2010 and January 2011, de-watered or deposited gravels in the majority of these sites, however, and the rivers were re-sampled to find suitable selective sampling reaches in late January 2011. Random samples were arranged along transects across the river bed including the selected sample reach (Figure 1). Seven suitable transects, two each in Cass and Godley Rivers and three in the Hopkins River, were found approximately one to two kilometres apart in each river. Temporal sampling sites were established, and random- and selectively-sampled points were fished between March and May 2011.

Selective sampling

Selectively-sampled reaches were fished at ten points longitudinally down reaches known to contain ULG from previous spot-fishing and site visits (Figure 1). Points were assigned randomly along a 100 m transect (Figure 1), with the distance from the bank for each point also randomly assigned. Randomly assigned points within 2 m of a previous assigned point were ignored, setting a minimum distance between samples. Selective-sampling was aimed at obtaining information on ULG abundance and habitat measurements from reaches where ULG were known to occur, so habitat variables were only measured at points containing ULG. Sampling was continued until ten points with ULG present were fished and measured. If ten points were not sampled in the first 100 m transect, then additional sampling points were randomly assigned upstream and downstream of the original reach.

Random sampling

Random samples were arranged along a transect perpendicular to, but also intersecting, the selectively-sampled 100 m reach (Figure 1). The starting location of this transect was randomly assigned along the selected reach, and points were fished along the random-sampling transect either side of the selectively-sampled reach, wherever the transect crossed active channels on the riverbed. Points were fished in each channel intersecting the transect and for channels greater than 2 m wide, multiple points were fished for every 2 m of channel width with the starting positions of fishing with respect to the bank randomly assigned. Sampling proceeded from a single bank and a measuring tape was placed across the channel by walking across the channel downstream from sampling locations to prevent disturbing adjacent sampling locations. All points in a channel were sampled consecutively and habitat variables measured afterwards to avoid disturbing sampling points before fishing. The spacing of fishing points was sufficient to minimise disturbance from adjacent samples and

where present, fish were often captured at all points in cross-sections of single braids, indicating that adjacent sampling had not greatly affected capture success.

Temporal sampling

Semi-permanent temporal sampling sites were established within selectively-sampled reaches to monitor changes in ULG abundance and the fish community through time. Locations of sampling sites were marked using GPS and site maps, and stage height loggers (WT-HR 1000, TruTrack, Christchurch, New Zealand) were installed to monitor flow changes over time. Sites were fished using the equipment described below in 30 m reaches closed with upstream and downstream nets. Reaches were fished on four occasions, dependent on weather and access, in April, July and October 2011, and finally in January 2012. Loggers were removed between January and April 2013 and the status of the reach was recorded upon removal as either wetted or dry. Closed reaches were fished for three passes and captured fish were removed from reaches for subsequent passes allowing an estimate of total numbers using closed-captures depletion estimation. Fish were identified and the natural total length of individuals was measured to the nearest millimetre. Total population estimates for reaches was calculated using closed-capture models in Program MARK (White and Burnham 1999) using the 'RMark' Package (Laake 2013) in R Program (R Core Team 2014). Reach area was measured on each sampling occasion and was used along with population estimates total to calculate densities for each species.

Fishing methods

Both selectively- and randomly-sampled sites were surveyed using spot electric fishing at points across transects with each riverbed. Each point was fished and habitat measurements were taken at the immediate fishing location. Points were fished using a backpack-mounted electrofisher (Kainga EFM 300, NIWA Instrument Systems, Christchurch, New Zealand)

over an area approximately two m^2 and fish were collected in a pole-seine held immediately downstream of fished areas by a second operator. Because conductivity varied from channel-to-channel across riverbeds, voltage was varied to keep electrical current in the water approximately the same. Electrical currents of ~ 300 mA were most effective and produced a desired galvano-tactic reaction towards the anode, with the fish swimming up from the substrate, without producing a tetany reaction before fish left the substrate. The presence of observers was unlikely to invoke any fleeing of fish prior to sampling because the fish are benthic and often in water with a broken surface, visually isolating them. Sampling effort was kept constant between all samples with the electrofisher operator and pole-seine width being kept the same throughout the study. Once captured, fish were identified, measured as for temporal sampling, and returned to the river.

Habitat variable measurement

Habitat measurements included water velocity, depth and substrate measures. Velocity was measured with a flowmeter (FloMate 2000, Marsh-McBirney Inc., Frederick, Maryland, USA) at points 0.5 m forward and to the centre of the pole-seine as well from each edge of the pole-seine at various depths through the water column in the centre of the sampling point to determine changes in velocity with depth. The measurements were used to produce a regression using log-transformed velocities and depth to estimate velocity at zero depth, giving an estimate of near-bed velocity (Gordon *et al.* 2004). Substrate was sampled from a point 0.5 m forward of the stop net using a 0.5 m square grid. Sixteen interescting points on the grid (based on 0.1 m grid squares) were sampled and each point was assigned to a class of substrate (sensu Harding *et al.* 2009). Substrate classes were assigned a weighted score and the mean weight of all substrates sampled at a point was calculated (similar to Jowett and Richardson 2008). Percentage cover of fines (sand and silt substrate classes) was estimated in

10 % increments based on the vertical coverage of fines over dominant substrate classes, equivalent to degree of embeddedness in fine sediments when calculating Brusven Substrate Index (Harding *et al.* 2009). Percentages were based on the height of fine coverage on larger gravels and cobbles, with completely covered substrates being assigned 100 % and uncovered substrates 0 %. Channel widths and channel slopes were recorded for each sampling point. Channel widths were measured as the entire width of wetted channel at the sampling point. Slopes were calculated using a 5 m level to calculate the drop in bed and water surface height at sampling points and then converted to degrees for analysis.

Statistical analyses

I used a principal components analysis to reduce the influence of multicolinearity amongst habitat variables (Dormann *et al.* 2013). Using only randomly-sampled points, habitat variables were mean-centered and standardised, and a principal components analysis (PCA) performed using the *prcomp* function in the *stats* package of the R program (R Core Team 2014). Principal components from PCA were then used to summarise habitat variables for further analysis. To avoid the influence of selectively-sampled sites in determining the dimensions of the principal components analysis, principal components scores were calculated separately for these samples. Principal components scores for selectively-sampled points were projected onto the same ordination space as randomly-sampled points using matched habitat variables to determine principal components scores for them based on the random-sample PCA.

Differences in habitat conditions between randomly- and selectively-sampled points were tested using principal components scores from points where ULG were present. Group differences in principal component scores for each sampling method were tested initially

using multivariate analysis of variance (MANOVA) and then investigated using separate ANOVA.

A binomial generalised linear model (GLM) using ULG presence as a response and component values from the PCA above as predictors was used to test for relationships between ULG occurrence and the habitat variables measured. All principal components were included in initial models and a best model was determined using stepwise model selection (McCullagh and Nedler 1989). Each term was systematically added or removed from models and tested against the previous iterations. Where the addition or removal of the variable did not significantly affect the model fit, a simpler model was selected, leaving only those terms with significant explanatory power in the model. Model fit was determined using Akaikes Information Criterion (AIC) values; decreases in AIC following the removal or inclusion represented greater model fit. Model selection was halted once further additions and removals no longer improved model fit. Reduced models are reported and the contribution of individual principal components was tested using significance tests based on the Chi-squared distribution.

Since habitat measurements were only taken at selectively-sampled sites for points where ULG was present, information on habitat variables was only taken for points with non-zero abundance of ULG. Therefore I used a zero-truncated count model (zero-truncated poisson GLM; Hilbe 2007, Zuur *et al.* 2009b) to test the relationship between ULG abundance and PCA component scores for selectively-sampled sites. Models were fit using the *VGAM* package (Yee 2013) in R program (R Core Team 2014) utilising the 'pospoisson' distribution. The number of points required to collect ten points of ULG presence varied across selectively-sampled sites, the *offset* argument of *vglm* function was used in the *VGAM* package to adjust the influence of each sampling point using average number of points

sampled to obtain a single ULG presence point for that reach. Model selection procedures were used to determine the influence of principal components following the same procedures as for the randomly-sampled points described above.

Results

Abundance of both, ULG, and all other fish species was variable, but eventually declined to zero at the majority of temporal sites within nine months (Figure 2). During sampling, sites were either, filled with deposited gravels, or de-watered as channels migrated. This channel alteration ended sampling early at all Cass River sites and occurred at sites (expect Hopkins-2, *see Discussion*) in other catchments within twenty months (Figure 2). Stage height measurements were patchy over time as loggers were buried or malfunctioned following inundation. Generally, stage heights varied over time at sites and recorded water heights in excess of 600 mm. At 600 mm stage heights, floods inundated entire survey reaches, and most of the riverbed, and were sufficient to detach loggers from fastenings and bury site markers and loggers.

The first two principal components from a PCA of habitat variables explained 50 % of the variation in the principal components. The first principal component (explaining 31 %; Table 1) was strongly negatively correlated with depth and velocity, and positively correlated with percent coverage of fines (Figure 3B). The second principal component (explaining 18 %; Table 1) was negatively correlated with water and bed slope (Figure 3B) and remaining axes explained half of the variation in the habitat variables (Table 1). A MANOVA of principal component scores showed no significant difference (Wilk's Lambda = 0.78, d.f. = 9, 58, P = 0.09) between selectively and randomly-sampled points for points where ULG were present suggesting that habitat conditions in selected sites were similar to those where ULG were found during random sampling (Figure 3A).

ULG were rarely encountered during random sampling of the riverbed. Only fifteen individuals from fourteen separate sampling points were captured from a total of 154 sampled points, equivalent to approximately 308 m^2 of riverbed (Table 2). Fish occurrence across randomly sampled transects was generally low, with a mean of 14.7 % of points sampled across the eight random transects containing fish (Table 2). ULG typically occurred in the absence of other fish species and were only found in sympatry at two out of 14 randomly-sampled points where they were present (Table 2).

Fish occurrence was greater at selectively-sampled sites; mean 38.6 % across the eight selectively-sampled transects. However, the occurrence of ULG in sympatry was also relatively low in selectively-sampled transects. ULG occurred with other species in 11 % of sampled points where fish were present. Collectively, selectively-sampled sites had greater mean percentage occurrences of ULG (31.4 %; Table 2) than randomly-sampled sites (8.1 %; Table 2). However, occurrence varied across both random- and selectively-sampled transects reflecting the highly patchy distribution of ULG. For example, the greatest percent occurrence of ULG in randomly-sampled reaches, 17.6 %, was larger than values for three of the selectively-sampled reaches (Table 2). Therefore, while there were overall differences in sampling success between randomly- and selectively-sampled transects, for some transects, these differences in capture success of ULG were negligible. Overall, ULG and other fishes were sparse across river beds and their distribution was highly patchy.

ULG occurrence was best explained ($\chi^2_{(1,101)} = 6.69$, $P < 0.01$) by the first principal component related to depth, velocity and percentage cover of fines with the probability of ULG occurrence increasing with the first principal component (Figure 4). Correlations for these axes show that the first principal component axis corresponded with decreasing depth and velocity values and increasing percentage fines (Figure 3; Table 1). Therefore, the

probability of ULG occurrence was highest in shallow, low-velocity habitats, with a high percentage of fines. High percentage fines was negatively correlated with both velocity (Pearson's R = -0.44, $P < 0.001$) and depth (Pearson;s R = -0.38, $P < 0.001$) and were characteristic of slow and shallow habitats.

No significant relationships were found between positive counts of ULG and any of the nine principal components I tested. A model containing the third principal component was the only model shown to fit the data better than the intercept-only model in both forwards and backwards model selection. However, differences in AIC score between these models was negligible and the best model was not significantly different from an intercept-only model ($\chi^2_{(1,56)} = 2.6$, $P = 0.11$). Therefore, I found no influence of the habitat variables I measured on ULG abundance in selectively-sampled sites suggesting that factors which influence their occurrence do not influence their abundance.

Discussion

I investigated habitat selection and the influence of flow disturbances on populations of a threatened fish, upland longjaw galaxias (ULG) in highly disturbed braided rivers. I monitored their populations at sites over time, and measured the availability and use of their habitats. The occurrence of ULG was patchy through time, as well as spatially across the riverbed. Over time, disturbances eliminated habitats which were previously occupied by ULG, reducing ULG and other fish populations at these locations over time. ULG and other fishes were sparse across the entire river bed, and a high proportion of sampled points across rivers were unoccupied and ULG occurrence, but not abundance, was positively related to relatively slow and shallow channels. These habitats were abundant, but frequently unoccupied by ULG across riverbeds indicating weak habitat selection and suggesting that their patchy distribution in braided rivers may not be caused by low habitat availability.

Habitat selection and population persistence

The patchy spatial and temporal occurrence of ULG in braided rivers, is likely driven by the very dynamic nature of habitats in these rivers, caused by large and frequent flow disturbances coupled with mobile beds (van der Nat *et al.* 2003). ULG occurred in these highly disturbed rivers, but I have shown they are sparsely distributed in microhabitats which are short-lived but abundant. Therefore, the persistence of ULG populations in these disturbed and constantly changing environments may rely on adaptations which allow them to survive in these habitats.

Extreme disturbances will still likely negatively affect fish species despite being suited to disturbed habitats. Fish communities are often altered by flow disturbances which remove species, but this seldom eliminates entire communities (Matthews 1986) and studies that report declines following floods are often conducted following especially severe disturbances (Schlosser 1982, Meffe 1984). Therefore, the declines in ULG observed during temporal sampling were likely linked to large disturbances which catastrophically altered those habitats previously occupied by ULG, depositing gravels, or de-watering channels following changes in the riverbed morphology (Plate 3). However, the elimination of these habitats does not necessarily suggest that ULG populations were also eliminated. Disturbances of the magnitude observed are common in these rivers, and have thus far failed to eliminate ULG in these rivers. Much more likely, is that ULG are able to move between suitable habitats as they are continually created and eliminated, and that the patterns observed during the temporal survey describe the fates of local habitat patches and not the fate of all habitats across the riverbed. These habitat 'patches' are the basis of patch dynamics, an important property of disturbed ecosystems (Pickett and White 1985, Townsend 1989) which affects how disturbances influence populations and their recovery from disturbances (Lake 2000).

Fishes can possess adaptations and strategies to avoid or withstand disturbances, but the efficacy of these adaptations and strategies for maintaining populations is likely to decline with increasing disturbance magnitude (Townsend, Scarsbrook and Doledec 1997, Lepori and Hjerdt 2006). Braided rivers are characterised by high channel movement which is sufficient to maintain un-vegetated alluvial riverbeds over one kilometre wide containing (usually > 5) channels. During high flows in these rivers the entire channel is inundated, and under such conditions unaffected habitat patches on the riverbed are unlikely (van der Nat *et al.* 2003). This leaves few opportunities for organisms in these rivers to use in-channel refugia because the availability and efficacy of local in-stream refugia declines with increasing disturbance magnitude (Sedell *et al.* 1990, Townsend, Scarsbrook and Doledec 1997). The wide extent of these disturbances may also increase the distance to sources of potential colonists from surrounding rivers (Detenbeck *et al.* 1992), restricting the recovery of fish populations. Furthermore, because fish biomass is linked to production of their invertebrate prey (Jellyman, Booker and McIntosh 2013), which declines with increasing disturbance (Death and Winterbourn 1995), overall fish biomass in these braided rivers may also be limited by low availability of prey. Thus, several mechanisms may drive the dynamics of fish populations in disturbed rivers and it is not at all surprising that fish populations were sparse, patchy and in generally low abundance.

The above concepts, low overall abundance, low refugia availability and distant proximity to refuges, combined with unpredictable, frequent and high magnitude disturbances, offer few options for fishes to escape negative effects of disturbances in braided rivers. This likely limits recovery from previous disturbances and causes communities in braided rivers to be in nearly constant states of early recovery. Moreover, the high spatial and temporal variability likely favours species, like ULG, which may be able to persist in disturbed environments which are free from competitors. Therefore, the composition of communities in these

extremely variable environments may be largely determined by the abilities of organisms to move between habitat patches as they change, forming 'mobility-controlled' communities (Townsend 1989). Possible movement by ULG between habitats, highlights an important question, which remains unresolved, about the spatial scale of any movement. Specifically it is unknown whether ULG move between habitats within braided rivers, between habitats in the wider catchment or both. If ULG move between habitats in the wider catchment, then they could occupy more stable spring and tributary habitats at certain times. They occur in springs adjacent to braided river main stems in several other catchments, but were only found in one site outside of the main braided river during this survey (described below).

Populations in spring habitats would be likely much more stable and may provide a steady source of individuals to recolonise the frequently disturbed braided main stems. Such downstream movement between habitats was suggested by Bonnett (1990), although the reason for such movements whether, downstream migration of mature individuals from springs to spawn in braided rivers, or downstream displacement of juvenile fish, remained unclear. Similarly, determining whether, stable spring-fed or disturbed braided channels are preferred habitats remains difficult because ULG are known to occur in both, and each habitat presents significant trade-offs for ULG populations. For example, in stable spring-fed habitats ULG populations would be less influenced by disturbances, but interspecific competition should increase, while in disturbed braided channels, interspecific competition would be lower but the effects of disturbance may be costly. Further investigation of the role of these differing habitats for ULG populations is crucial, but will require much more detailed investigation of their populations over time and in catchments where both habitat types exist.

For organisms, like ULG, to be able to occupy or recolonise extremely disturbed habitats there has to be some specific traits which facilitate persistence. In particular, generalist habitat preferences are predicted to promote recolonisation of organisms in disturbed rivers and enable organisms to occupy a wide range habitats (Townsend, Doledec and Scarsbrook 1997). Through this they may avoid habitat competition and would be able to occupy changing habitats for longer duration or such traits may assist them in recolonising a range of wide habitats following disturbances. ULG used a broad range of habitats, with their presence being highest in shallow and slower habitats. These preferences of ULG match previous descriptions of their habitat (Bonnett 1990, McDowall 2006) and habitat preferences (Jowett and Richardson 2008). Such habitats are common across braided rivers and remain common even over a wide range of discharge (Mosley 1982). Furthermore, because habitat proportions in unregulated braided rivers remain relatively constant over time despite changes in, location (van der Nat *et al.* 2003), these habitats are likely to remain common following disturbances. If generalist habitat preference in ULG is part of a suite of characteristics which promote survival or recolonisation of frequently disturbed habitats, then further traits, so far unknown for these fish, but typical of disturbance-tolerant fishes may also be important (Townsend, Doledec and Scarsbrook 1997).

Conservation implications

In the absence of limits on available habitat and overall low fish densities, competition in disturbed rivers should be low. This lack of competition should suit those native fishes which are typically poor competitors against more widespread native and exotic competitors such as koaro (*Galaxias brevipennis*) and salmonids respectively. However, the high availability of habitat and low overall fish densities that favour ULG in these rivers are maintained by the severe disturbances which characterise unmodified and unregulated braided rivers. Therefore,

changes to flow regimes or geomorphic modifications which reduce the severity of these disturbances are likely to affect species, like ULG, which occur in these environments and likely benefit from reduced interspecific competition. If the severity of disturbances was to decrease in these rivers, then they are likely to become more suitable for competitively-dominant fishes, increasing competitive interactions which would likely have adverse effects on ULG populations. Conservation efforts for ULG should therefore focus on maintaining the disturbance regimes which structure their populations and the surrounding fish communities.

In addition to characteristics which promote *in-situ* survival during disturbances, fish also use refugia to avoid disturbances (Sedell *et al.* 1990, Davey, Kelly and Biggs 2006). Recovery of populations is often dependent on aspects of the surrounding rivers and the ability of the fauna to recolonise from adjacent habitat refugia or, if the effects of a disturbance are patchy, then from unaffected patches (Townsend 1989, Woodford and McIntosh 2010). For some refugia, this may require fishes to actively move to occupy these refugia. For these fishes, maintaining the availability and connectivity of refugia habitats will be especially important. Galaxiids, for example, are known to burrow through loose gravel substrates and hyporheic connectivity is likely important for their survival in drying streams (Dunn and O'Brien 2006). If this refuge is also used for avoiding high flows by ULG, then changes which reduce this connectivity, such as bed armouring or increased sedimentation, may affect access to this refuge. Therefore, maintaining connectivity between these habitats will be important for maintaining the availability of these habitats as refugia.

I found some evidence of peripheral habitats being used by ULG in this survey. During site visits a single short reach (~ 2 m in length and 0.4 m wide) which flowed from a small spring on the upper banks of the main stem of Hopkins River (Plate 4) was located which contained a density of ULG far greater than those in the surrounding riverbed. Re-surveys of this site

over time (Hopkins-2; Figure 2) showed the reach was not continually occupied by ULG, and may have been used only seasonally, as either a refuge or for spawning, but their reason for using these habitats is unknown. The role of such habitats and their distribution (the reach in this study was only found coincidently) is yet to be determined but given the extensive searching of the riverbed and floodplain spring creeks (see Chapter Two), I am reasonably certain they are rare. However, movement between disturbed main stem habitats and stable peripheral habitats might be expected given the highly disturbed braided environments ULG inhabit. Although use of such habitats will be difficult to study, it will be important to determine their role in facilitating ULG population persistence.

Habitats peripheral to main stems can be important in a meta-population context as sources of recruits for galaxiid populations (Woodford and McIntosh 2011). If peripheral habitats such as perennial spring habitats are important source populations of ULG individuals, then main stems could act primarily as sink habitats. Alternatively, if such springs are used mainly as spawning habitats, then they should provide a relatively steady source of recruits in comparison to any spawning which might occur in disturbed main stems. Such habitats are particularly important for fish communities and meta-populations over large scales (Falke and Fausch 2010) and the potential role of these peripheral habitats is great, whether used as refugia, or for spawning, and determining their function should improve management for ULG.

The current study was challenged to varying degrees by low abundance of ULG, frequent disturbances removing sites and equipment, and the large size of the rivers I worked in. Despite attempts to alter survey design to sample larger numbers of ULG using selectively-sampled sites, relatively few ULG were captured. Furthermore, capture success was variable among selectively-sampled sites, and in some cases, was no more successful than random

sampling. The large changes in ULG populations I observed over time along with their wide habitat preferences and the changing physical character of riverbeds means fish populations and habitats would be expected to change over time. Thus, although monitoring of a rare fish like ULG is important, innovative and flexible sampling designs will be needed to effectively monitor them in these ever-changing environments. Further investigation of key habitats which may be used only occasionally by ULG as refugia or spawning sites, would likely fill gaps in our current knowledge of this species and may be critical to population persistence. If these more stable and isolated habitats exist, and their functions for fish populations are determined, then targeted conservation efforts and monitoring of these habitats would be a priority.

This study adds to a limited literature on rare and little-known New Zealand galaxiids, which for ULG has included life history and diet studies (Bonnett, Sagar and Docherty 1989, Bonnett 1990, Bonnett 1992) and estimates of habitat preferences (Jowett and Richardson 2008). However, given the widespread and continued use of habitat models requiring habitat preference information for management and conservation decision-making in New Zealand, additional information on the habitat requirements of these rare fish would likely aid their management. Equally, my results highlight some of the limitations of these models for highly-dynamic and disturbed habitats (Lancaster and Downes 2010). For example, in rare fishes, even targeted approaches may fail to sample abundance in rare fishes with patchy distributions, and may instead have to rely on presence-absence information. The use of habitat requirements for management should strongly consider the limitations of the sampling in habitat studies. Moreover, an increased knowledge of spatial population dynamics is needed to determine what roles particular habitats play for fish community persistence across disturbed rivers.

This study highlights the extreme spatial variability of ULG populations across floodplains in braided New Zealand rivers. This, coupled with the extreme variability of flows and the continual spatial reconfiguration of braided riverbeds during floods, makes populations of ULG extremely vulnerable, as well as difficult to monitor and study. Current information on the species is largely assumed from limited observations of these fish, and this is likely to continue to influence their conservation status. Although considerable logistical challenges need to be overcome, if populations of rare fish in highly disturbed habitats are to be secured, then the importance of spatial dynamics, and potential for meta-population dynamics need to be understood.

Tables and Figures

Table 1. Summary of principal components analysis based on habitat variables collected during the sampling of randomly selected points across riverbeds at seven locations in braided rivers.

Principal component [a]	Factor correlations [b]	Eigen value	% variance explained	Cumulative % variance explained
PC1	-: depth, velocity, near-bed velocity +: % fines	2.83	0.31	0.31
PC2	-: bed slope, water slope, substrate heterogeneity	1.63	0.18	0.50
PC3	-: substrate coarseness	1.21	0.13	0.63
PC4	+: width	1.10	0.12	0.75
PC5	-: substrate hererogeneity	0.89	0.10	0.85

[a] Principal components which explain ≥ 10 % of the variance in habitat variables.
[b] Variables listed correlate with a principal component at Pearson's correlation coefficient > 0.5; '+' and '−' indicate positive or negative correlation.

Table 2. Occurrence of upland longjaw galaxias (ULG) and non-ULG species (non-ULG) for random- and selectively-sampled transects. Totals and means are shown in bold, and are based on eight transects for random- and selectively-sampled transects. Totals are summed values for numbers of fish captured and number of points where a taxon was present, and mean values for % occurrence.

			Number of fish captured			Number of points present							% occurrence					
									allopatry		sympatry					allopatry		sympatry
River	Transect	Sampling method	ULG	non-ULG	all species	ULG	non-ULG	all species	ULG	non-ULG	all species	Points sampled	ULG	non-ULG	all species	ULG	non-ULG	all species
Cass	1	random	0	1	1	0	1	1	0	1	0	17	0.0	5.9	5.9	0.0	100.0	0.0
	2		7	3	10	6	2	7	5	1	1	34	17.6	5.9	20.6	71.4	14.3	14.3
Godley	1		2	3	5	2	2	4	2	2	0	20	10.0	10	20.0	50.0	50.0	0.0
	2		2	5	7	2	4	5	1	3	1	23	8.7	17.4	21.7	20.0	60.0	20.0
Hopkins	1		2	3	5	2	2	4	2	2	0	20	10.0	10	20.0	50.0	50.0	0.0
	2		1	2	3	1	1	2	1	1	0	21	4.8	4.8	9.5	50.0	50.0	0.0
	3		1	0	1	1	0	1	1	0	0	19	5.3	0	5.3	100.0	0.0	0.0
All transects			**15**	**17**	**32**	**14**	**12**	**24**	**12**	**10**	**2**	**154**	**8.1**	**7.7**	**14.7**	**48.8**	**46.3**	**4.9**
Cass	1	selective	14	0	14	13	0	13	13	0	0	24	54.2	0.0	54.2	100.0	0.0	0.0
	2		19	36	55	13	20	26	6	13	7	69	18.8	29.0	37.7	23.1	50.0	26.9
Godley	1		19	0	19	10	0	10	10	0	0	11	90.9	0.0	90.9	100.0	0.0	0.0
	2		12	3	15	10	2	11	9	1	1	42	23.8	4.8	26.2	81.8	9.1	9.1
Hopkins	1		10	18	28	10	16	26	10	16	0	145	6.9	11.0	17.9	38.5	61.5	0.0
	2		11	16	27	9	12	20	8	11	1	98	9.2	12.2	20.4	40.0	55.0	5.0
	3		12	11	23	10	9	14	5	4	5	62	16.1	14.5	22.6	35.7	28.6	35.7
All transects			**97**	**84**	**181**	**75**	**59**	**120**	**61**	**45**	**14**	**451**	**31.4**	**10.2**	**38.6**	**59.9**	**29.2**	**11.0**

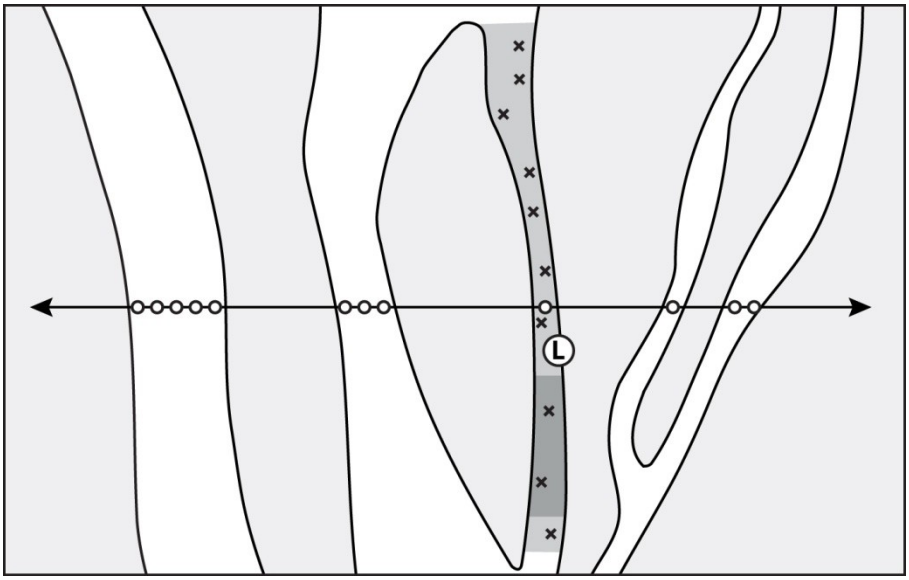

Figure 1. Diagram of selective- and random- and temporal-sampling layout. Wetted channels are shown as white and the surrounding riverbed is shaded light-grey. Sampling points for the random-sample are shown horizontally along the lateral transect and sampling points are represented by open circles. Arrows at the ends of the random-sampling transect represent further random-sampling points taken across the riverbed but not shown in the diagram. Sampling points for selective-sampling are shown as crosses and the selectively-sampled reach is shown as the mid-grey shaded region arranged longitudinally in one reach. The location of the temporal-sampling reach is shown within the selectively-sampled reach and is shaded dark grey and the position of the stage-height logger is shown as the open circle labelled (L). Flow direction is from top to bottom of the diagram.

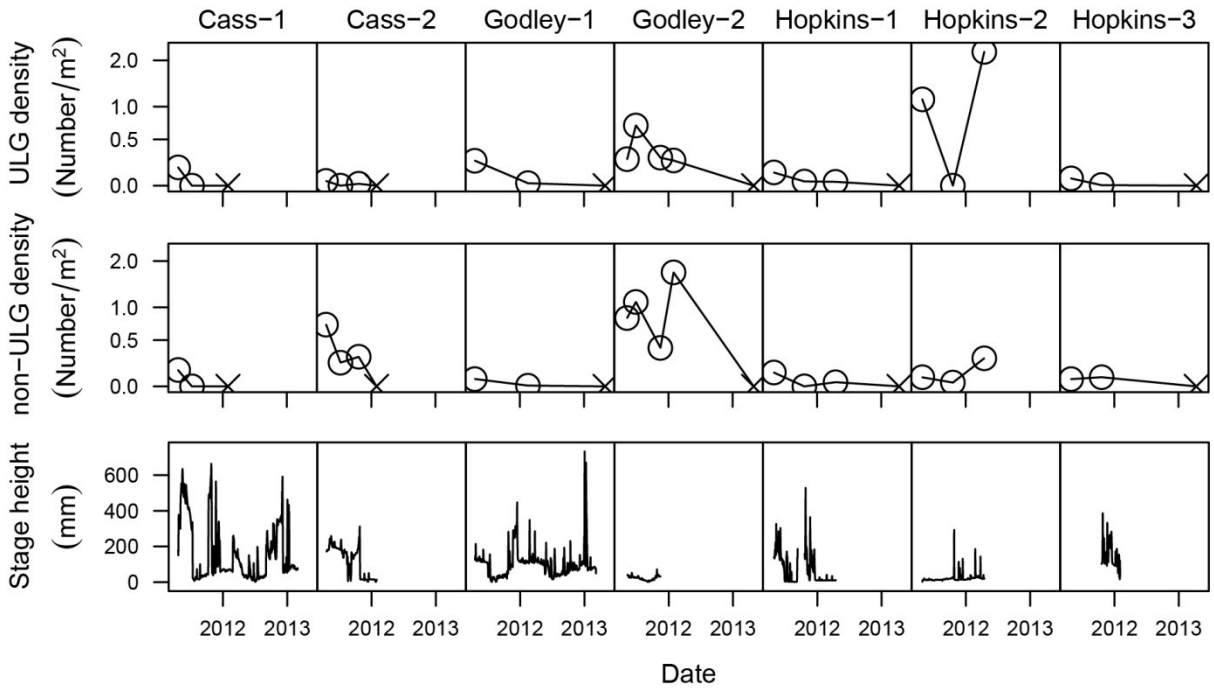

Figure 2. Upland longjaw galaxias abundance and stage height over time in seven upper Waitaki River braided river sites. Circles represent densities of ULG and other fishes under wetted conditions and crosses represent conditions where the stream was dry and could not be sampled. Abundances are shown on log-axes.

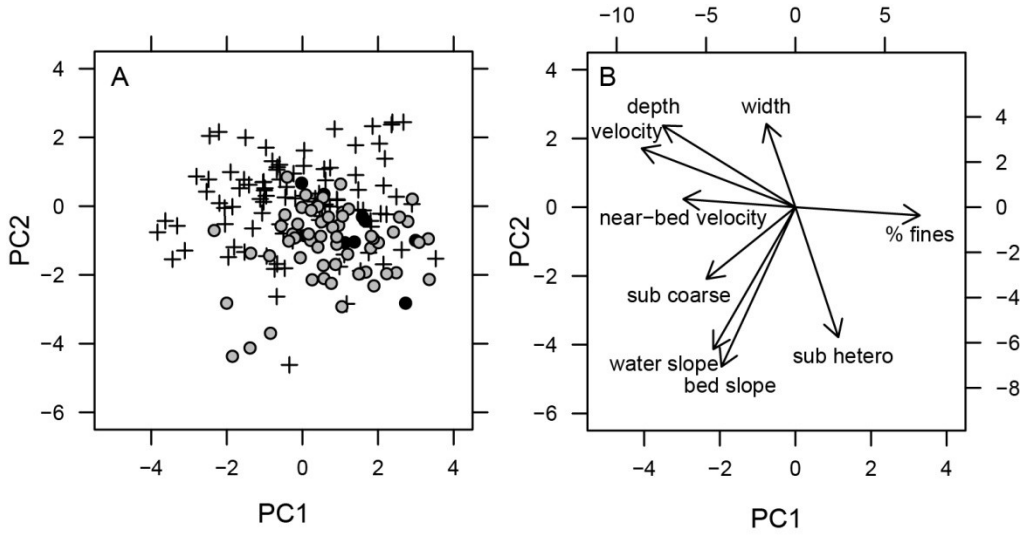

Figure 3. Biplots of the first and second principal components showing upland longjaw galaxias presence and absence (A) and vectors of physical habitat variables (B). In (A), circles represent sampling points where ULG were present during random- (black filled circles) and selective-sampling (grey filled circles), and crosses represent points where ULG were absent from random-sampling. In (B) the relative contribution of habitat variables to principal components is shown on the same scales as principal components, and arrow length represents the relative proportion of variance explained for that principal component and direction shows which axis variables were most associated with and positive and negative values represent increasing or decreasing relationships.

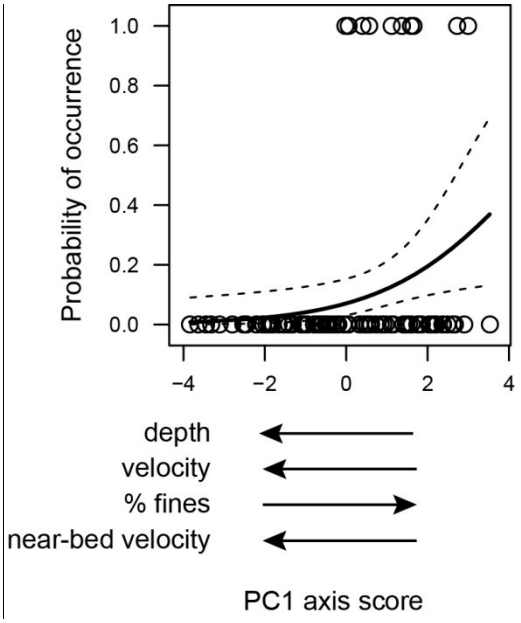

Figure 4. Probability of upland longjaw galaxias occurrence in randomly-sampled points in relation to physical habitat measures derived from principal components analysis. The principal components analysis was based on random samples of habitat variables collected from a cross-section of braided river habitat at seven points. Sampled points are shown as open circles and fitted occurrence probabilities (solid line) and 95 % confidence intervals (dashed lines) were obtained from binomial regression of principal components and principal components shown above were selected using forwards and backwards model selection.

Plate 3. Photographs showing changes at temporal sampling sites following high flows in Cass River: Gravel deposition at the Cass-1 site in October-2011 during flooding (upper left) and following flooding in January 2012 (upper right); Dewatered channel at Cass-2 site in April 2012 prior to dewatering (lower left) and following dewatering in January 2012 (lower right). Arrows indicate the location of stage height recorders for comparison.

Plate 4. Photographs of location of seasonally occupied upland longjaw galaxas (*Galaxias prognathus*) habitat alongside a main stem channel in Hopkins River (Hopkins-2). View of reach in relation to main stem (left) and close-up of reach (right) with arrows indicating the location of the small reach in both photographs.

Plate 5. Bignose galaxias (*Galaxias macronasus*) are endemic to a single large South Island catchment, the upper Waitaki River, where they are usually found in slow-flowing streams associated with wetlands or springs.

Chapter Four:

Flow-mediated antagonistic interactions reduce populations of a threatened habitat specialist fish.

Introduction

Global climate changes are predicted to alter the timing and intensity of climatic events, ultimately causing widespread changes to abiotic conditions in ecosystems (Heino, Virkkala and Toivonen 2009, IPCC 2013). Such changes are likely to impact the functioning of ecosystems and their components by altering species abundances and distributions (Heino, Virkkala and Toivonen 2009, Van der Putten, Macel and Visser 2010, Walther 2010). The outcomes of such influences for individual species are likely to depend on characteristics of both the ecosystem, including other species, and of the focal species themselves. Species traits are under selection to optimize reproductive success (Southwood 1977, Lytle 2001) under the habitat 'templet' an organism typically occupies. Alteration of the arrangement of these templets in ecosystems forces changes in either species distributions, or reproductive success and may therefore be one of the biggest consequences of global climate change (Hulme 2005). Such influences could be particularly severe for specialist species and for those in ecosystems influenced by invaders. Here, I investigated the responses of a spring-head specialist to current variation in flows to determine how changes in flow will affect their populations and influence invasive species which currently limit their distributions.

Specialist species, those which are able to inhabit rare or harsh habitats unfavourable for other species, benefit from such specialisation because they can often escape the effects of interspecific interactions. The range of environmental conditions that maintain suitable habitats for specialist species are typically narrow, and because the ranges of conditions

which maintain them can be easily exceeded with less overall change, the effects of changing environmental conditions will likely disproportionately affect such habitats. Therefore, specialised species, reliant on narrow ranges of environmental conditions, may be especially susceptible to global climate change.

Specialist species occupying freshwater ecosystems may be particularly vulnerable to climate changes (Ficke, Myrick and Hansen 2007, Heino, Virkkala and Toivonen 2009). The flow regimes of rivers are strongly driven by the timing and frequency of precipitation and temperature (Poff and Zimmerman 2010) and both are expected to be strongly affected by global climate changes (IPCC 2013). Furthermore, freshwater organisms, communities, and ecosystem functioning are strongly influenced by the prevailing flow regime (Marchetti and Moyle 2001, Lytle and Poff 2004, Biggs, Nikora and Snelder 2005), changes to flow regimes are likely to have large consequences for freshwater ecosystems across all levels of organisation, but especially for specialised species.

New Zealand non-migratory galaxiids are likely to be especially vulnerable to flow-related habitat change because they include a range of specialist species that are highly threatened and vulnerable to interspecific interactions. Non-migratory galaxiids are often restricted to habitats with few interspecific competitors and predators, and their non-overlapping distributions with both introduced (salmonid) and native (koaro) generalist species suggest they have inferior competitive ability outside of specialist conditions (Minns 1990, Townsend and Crowl 1991, Allibone 1999). Their common competitors are often generalist invaders, with broad habitat requirements and strong competitive abilities which allowing them to dominate communities when introduced to new habitats in receiving ecosystems. For example, introduced trout have been highly successful invaders in New Zealand. The assisted trout invasion has meant they now occupy many streams where only galaxiid fishes had

previously occurred, and owing to their highly competitive nature and large size they often either competitively exclude or prey on galaxiids, to the degree that their distributions seldom overlap (Woodford and McIntosh 2010). Native generalist fishes include koaro (*Galaxias brevipinnis*) and banded kokopu (*Galaxias fasciatus*). They are diadromous, have a large geographic distribution, occur in a wide range of habitats and can obtain a relatively large size compared to the fishes they typically exclude.

Generalists and/or invaders can be especially susceptible, however, to extreme natural disturbances for which specialist species are adapted (Meffe 1984, Bernardo *et al.* 2003), leading to differential effects of disturbances on generalist and specialist species. For example, specialist galaxiid species can persist through disturbances which otherwise remove generalist species such as non-native salmonids and generalist galaxiids (Closs and Lake 1996, Leprieur *et al.* 2006, McIntosh *et al.* 2010). Altered flows are likely to differentially affect populations of specialist fishes and of their generalist competitors. Therefore, it is important to investigate the effects of changing flows on specialists as well as their generalist competitors.

Aims and Objectives

In this study I aimed to determine how populations of a spring-head specialist non-migratory galaxiid, bignose galaxias, and their likely competitiors were affected by flow alterations. Bignose galaxias (*Galaxias macronasus*) are a recently discovered New Zealand galaxiid (McDowall and Waters 2003). The galaxiids (Family: Galaxiidae) comprise over half of New Zealand native freshwater species, but eleven of the twelve species classified as threatened are galaxiids (Goodman *et al.* 2014). Bignose galaxias are among those threatened species, classified as Nationally Vulnerable, largely due to their restricted range, which encompasses a single large catchment, the Waitaki River (Goodman *et al.* 2014). I predicted that given

bignose galaxias occur primarily in springs, their populations should be affected by changes in flow. Conditions during high and low flows may become unsuitable either for them or their competitors, but because bignose galaxias are associated with lower velocities I predicted that bignose galaxias abundance would decline with increasing flows (H1). Given the negative effects of salmonids and koaro on non-migratory galaxiids, and that their populations are often reduced following flow-related disturbances, I predicted that flow-related disturbance could reduce populations of these potential competitors (H2), and that bignose galaxias abundance would be greatest in streams with low salmonid and koaro populations (H3). Since the abundance of other, potentially competing, galaxiid species may also be affected by flow changes, I predicted that bignose galaxias abundance would be highest in streams with low abundance of other galaxiid species (H4). Thus, overall I expected generalist species (salmonids and other non-bignose galaxiids) to dominate the specialist bignose galaxias, and that flow would mediate any antagonistic interactions between them.

Methods

Survey Description

Clusters of study sites were established in spring-fed streams of two catchments of the Upper Waitaki River, South Island, New Zealand. In each of the catchments of the Ahuriri River (NZMG: 5658375N, 2239405E) and Fork Stream (NZMG: 5700170 N, 2296570 E), five springs were selected to establish a gradient of discharge and flow disturbance likely to influence bignose galaxias habitat. Previous discharge records were unavailable, so other evidence of previous flow disturbances (i.e. undercut banks, deposited debris on upper banks and scouring in the active channel) was used to guide selection. Generally, springs closest to large braided sections of river had more evidence of flow disturbances compared to hillslope springs which tended to be more stable. Fishing sites were selected so that sites were

relatively independent (i.e. neither upstream or downstream from one another and separated by stream distances of > 250 m).

At the start of the study (February 2011) all sites were flowing and based on preliminary site visits, all contained bignose galaxias. Several sites which had no evidence of past disturbances were assumed ground-water influenced and therefore more stable. Both catchments consisted of long, glacially-formed valleys, with a single large braided riverbed. Sites, with the exception of a single site in Fork Stream, were situated in channels peripheral to the main braided river. These channels all had a high degree of ground-water influence and were fed from either the bases of shingle screes, shingle fans or wetlands, or were adjacent to the braided river, and were presumed to gain subterranean flow from the main channel. In channels immediately adjacent to braided sections there was evidence that during high flow in the braided channel over-land flow could occur and high flows could occur in otherwise small, low-flow channels. Thus, although sites were all low-flow springs, there was considerable scope for some to be influenced by flow-related disturbances, high during floods and low during droughts, creating a natural experiment.

Sites were marked and sampled on six occasions between February 2011 and February 2013: February 2011, June 2011, October 2011, February 2012, April 2012 and finally on February 2013.

Habitat measurements

For the duration of the study discharge was recorded using stage height recorders and stage-discharge relationships constructed for each site. Discharge was estimated using area-integrated velocity measurements at eight equally spaced positions along cross-sectional transects (Gordon *et al.* 2004). Three transects were measured at each site at the upstream and downstream ends and the midpoint of each site. Velocity was measured using an electro

magnetic flow meter (Flo-Mate 2000, Marsh-McBirney Inc, USA) mounted on a wading rod .above the stream bed at a height 40 % of the water depth. The area of each reach was recorded during sampling by measuring wetted stream width at regular intervals to determine a mean width and multiplying by the length of a site. Additional intervals were taken and diagrams used to record wetted area for complex channels which ceased flowing and became fragmented pools.

Fish sampling

Fish were sampled using a backpack-mounted electrofisher (Kainga EFM 300, NIWA Instrument Systems, Christchurch, New Zealand) in stop-netted reaches. Fishing by a two-person team proceeded downstream with fish collected primarily in a pole seine (0.9 m width) held downstream from the electrofisher operator and secondarily in a large downstream seine net (both 4 mm mesh) fixed to each bank. Multiple fishing passes (2-3) were conducted at each site on each sampling occasion, where fish on successive runs were removed and abundance determined using closed-capture estimates, described below.

Statistical analysis

The number of fish in each reach was estimated using the R-Mark package (Laake 2013) in R program (R Core Team 2014) to obtain estimates using Program MARK (White and Burnham 1999; version 7.1). An equal capture probability was assumed between each pass, and emigration and immigration were set to zero reflecting a closed reach between passes. Estimates of fish numbers per reach were used, along with fish weights, to estimate a total biomass per species for each sampled site per sampling occasion. Where estimated fish numbers were equal to captured fish numbers, then total biomass was the sum weight of all captured fish. When estimated fish numbers exceeded captured fish numbers, additional biomass was estimated by multiplying the mean fish weight for a site by the difference

between estimated and captured fish numbers. Biomass estimates were used instead of density estimates, because the latter was likely to overestimate the effects of numerous small fishes and underestimate the effects of large-mass low-abundance fishes such as trout. For statistical analysis two datasets were used to represent fish populations both through and across time: the first comprised 'per sample' biomass estimates for each site and each sample through time, whereas the second comprised a mean of all biomass estimates from each site across time.

Using biomass estimates from across sites and through time, the influence of discharge on bignose galaxias biomass and total biomass of other fishes was examined using linear regression and mixed effects linear models. To test the effects of varying discharge on bignose galaxias using the gradient of discharges across sites, a mixed model treating sampling occasions as replicates was used to test the relationship between discharge and bignose galaxias biomass within each sampling period. Within-site, repeated-measures, analyses using sites as replicates, were unable to be tested because bignose galaxias biomass varied seasonally across all sites (Figure 1). Bignose galaxias biomass and discharge were log-transformed to reduce the influence of extreme values and improve model fit. The structure of the random effects was chosen by testing each random effect structure (alternatives included: random slope-fixed intercept, and random slope-random intercept models) without independent variables and assessing model fit using AIC values to determine the best random effects model (Zuur *et al.* 2009a). Once a random model structure was determined, the independent variable discharge was added. Model improvement was assessed using ANOVA to test the contribution of discharge to model fit based on a Chi-squared distribution.

The effects of mean discharge over the entire study on the mean biomass of bignose galaxias and their competitors at each site were assessed. Mean discharge was calculated over the entire study period for each site and corresponding biomasses were calculated for mean bignose galaxias biomass and mean biomass of non-bignose galaxias fishes. Additional predictors, mean velocity and median substrate diameter for each site, were also assessed. The total number of days a channel was dry and the frequency of flows greater than three times the median flow (FRE3) were also determined for each site to test the influence of drought and flood conditions, respectively. Relationships between bignose galaxias and non-bignose-galaxias biomasses and predictors were tested using linear regression on log-transformed dependent and independent variables. The effects of likely competing species, and species groups, were assessed using mean biomass for each site from across all samples. Means were calculated for bignose galaxias, alpine galaxias, trout (combined *Salmo trutta* and *Oncorhynchus mykiss*), total galaxiid (all galaxiids) and total non-bignose galaxias biomass. Relationships were tested using linear regression on log-transformed biomasses. The effects of alpine galaxias, trout and all non-bignose-galaxias on bignose galaxias biomass were assessed and the effects of trout biomass on total galaxiid biomass were assessed.

Flow manipulation experiment

Following initial field surveys, a flow-manipulation experiment was carried out in Fork Stream springs to determine the short-term effects of changes in flow on localised fish populations. A series of large baffles were used to alter flow in natural channels in Fork Stream. Baffles were made from untreated plywood sheeting joined together to divide the stream channel into two equal sides and fixed to the streambed using steel stakes. Discharge was reduced by diverting flow in front of a randomly selected channel side using an angled length of plywood sheeting at the upstream end. Four baffle-type treatments were used: (1) a

reference condition control reach without divided sides and no baffle, (2) a reach with divided sides but no baffle, (3) a reach with divided sides and baffles and (4) a reach with divided sides, a baffle and weirs down the reduced discharge side to further reduce discharge. Treatment order was randomly assigned and baffles were installed along stream sections spaced at least 50 m apart. Three replicate treatment blocks, each in separately fed springheads, were initially installed. The uppermost treatment block stream dried completely and unexpectedly during the experiment. Alternative replicate streams were either unsuitable or also dry, so instead a second trial of existing locations, but with flipped treatments was conducted. Reduced discharge channels were swapped for channels with increased flows so that the flow was reduced on the opposite side of the channel than that in the initial trial. Trials commenced immediately following the installation of baffles and ran for sixteen and nineteen days each for the first and second trials, respectively from 8th March to 25th March 2013 and from 16th April to 6th May 2013.

During the experiment fish populations already present in streams were allowed to move between increased and reduced flow channels, and between fence treatments, before being sampled from each channel separately at the end of trials using multi-pass closed-reach electrofishing as described above. However, because the electrofishing of one channel side was likely to influence fish movement on opposite sides, both sides were fished simultaneously by moving between sides while fishing downstream. Length and weights of captured fish were measured as above, and estimates of total fish numbers were calculated using closed capture estimates in Program Mark (described above). Discharge, mean channel depth, wetted channel width and wetted area were measured and calculated for each treatment side, and for each trial, and differences in discharge, depth and velocity between treatments and increased and reduced flow sides were tested using ANOVA and Tukey pairwise comparisons, with each treatment block and trial treated as replicates.

The influence of discharge manipulation treatments was tested using the ratio of fish biomass in reduced-discharge channel to increased-discharge channels for each treatment. Reduced and increased discharge sides for control treatments (divided reaches but with no baffle) were assigned based on observed discharges. Treatment differences in biomass ratio were log-transformed and tested using ANOVA treating blocks and trials as replicates and Tukey pairwise comparisons were used to identify significant treatment differences. Differences in bignose galaxias biomass between reference (no divided sides or baffle) and fence-control (divided sides and no baffle) treatments were tested using a paired t-test. Treatments were paired according to block and trial and combined biomass between channel sides was used for fence controls as reference control reaches were not divided.

Results

There was a gradient of discharge across sites over the course of the study (Figure 2), with high and low discharges occurring at many sites as well as relatively stable flows in some. Surprisingly, many of the streams which contained bignose galaxias in initial samples subsequently dried and this was the case even in sites which exhibited relatively stable flows prior to drying (Figure 2). Large changes in discharges were matched by large changes in bignose galaxias biomass, while bignose galaxias biomass remained relatively constant in sites with negligible changes in discharge (Figure 2).

Alpine galaxias were found in eight sites, especially following high flows at the start of the study (Table 1). Canterbury galaxias were found at seven sites, but were typically at low densities compared to other galaxiids (Table 1). Upland longjaw galaxias occurred at only two sites and were rare (Table 1). Trout were present in almost all sites which did not dry, but often in low biomass. Upland bully were found in one site (Table 1), and their biomass was negligible so they were excluded from further analysis.

Bignose galaxias biomass declined with increasing discharge ($\chi^2_{(1,4)} = 4.08$, $P = 0.043$; Figure 3). This negative relationship occurred in five out of six sampling periods and was largely consistent across samples although was especially pronounced during sampling periods where the gradient of discharge across sites was strongest (Figure 3). Mean habitat conditions throughout the study had a strong influence on both bignose galaxias and non-bignose galaxias biomass over time. The mean combined biomass of non-bignose species was strongly positively related to mean discharge across all sites ($R^2 = 0.61$, $P < 0.02$, ; Figure 4A), whereas the mean biomass of bignose galaxias declined with increasing discharge, although this relationship was only on the verge of being significant ($R^2 = 0.42$, $P = 0.08$). Biomass of non-bignose galaxias fishes increased with mean velocity ($R^2 = 0.48$, $P = 0.06$; Figure 4B), though this relationship was only nearly significant whereas, bignose galaxias biomass was not influenced by mean velocity ($R^2 = 0.31$, $P = 0.2$; Figure 4B). There was a significant positive relationship between mean bignose galaxias biomass and mean median substrate diameter ($R^2 = 0.54$, $P = 0.03$; Figure 4C) but similar relationships were not found for biomasses of non-bignose galaxias biomass (Figure 4C). There were no relationships between bignose galaxias, or other species biomass and measures of high (frequency of discharges over three times the median flow; FRE3) and low (total dry days) flow disturbances (Figure 4D, Figure 4E).

There were strong relationships across sites between the mean biomass of bignose galaxias and all other fishes, and between the mean biomass of all galaxiids and salmonids (Figure 5). Although no significant relationships were found between bignose galaxias and salmonids (Figure 5B) and alpine galaxias (Figure 5C). Mean bignose galaxias biomass was lower when associated with higher mean biomass of non-bignose galaxias ($R^2 = 0.64$, $P = 0.02$; Figure 5A) and mean total galaxiid biomass also was lower when mean trout biomass was high ($R^2 = 0.96$, $P < 0.01$; Figure 5D).

In-stream discharge manipulations were successful in altering discharge in experimental channels. Discharge was significantly altered between reduced and increased flow sides ($F_{(3,12)} = 19.7$, $P < 0.001$) in baffle-only treatments ($P < 0.01$) and baffle and weir treatments ($P < 0.001$). There were no treatment differences between baffle-only and baffle and weir treatments for reduced flow ($P = 0.27$) or increased flow sides ($P = 0.95$). Velocity and depth were strongly correlated with discharge for flow-altered treatments (Pearson's $R = 0.83$ and 0.72, respectively) so only discharge ANOVA are shown.

There were significant treatment effects on the ratio of bignose galaxias biomass between reduced and increased discharge channels across all treatments ($F_{(2,9)} = 7.3$, $P = 0.013$; Figure 6A). Pairwise tests showed that the greatest differences in the ratio of bignose galaxias biomass between reduced and increased channels was between control and fence – no weir ($P = 0.014$) and control and fence – weir ($P = 0.044$) treatments. No significant differences were found between the two discharge-altering treatments ($P > 0.7$; Figure 6A) suggesting there was no effect of weirs on bignose galaxias biomass. There were no significant differences between control treatments with and without fences ($t = -2.61_{(df=3)}$; $P = 0.08$; Figure 6B), suggesting there were no detectable effects of installing fences in the stream on bignose galaxias biomass ($t = -2.61_{(df=3)}$; $P = 0.08$; Figure 6B).

Discussion

The patterns found in this study could be explained both by niche differences between bignose galaxias and other fishes, and by antagonistic interactions between bignose galaxias and likely interspecific competitors and predators. Bignose galaxias and their likely competitors may occupy low-discharge and high-discharge niches respectively. Alternatively, discharge may only directly influence populations of one species, but interactions between these may influence populations of other fishes. For example, populations of other fishes may

be influenced by discharge and may indirectly influence bignose galaxias populations. I found evidence for differential use of low and high discharge habitats by bignose galaxias and other fishes in both field surveys, where mean biomass of bignose galaxias declined with discharge while biomass of other fishes increased with discharge, and also in the discharge-manipulation experiment, where bignose galaxias occupied slower habitats over faster habitats. However, the mechanisms for higher occupation of slow habitats remain unclear and again could be explained by both discharge-related niches of species or by antagonistic interactions whereby other fishes exclude bignose galaxias from fast habitats, which would explain the reduced biomass of bignose galaxias in streams with high biomass of other fishes.

Both surveys and the stream manipulation show that bignose galaxias appear able to occupy low-discharge habitats and may selectively occupy such low discharge habitats. During surveys I observed bignose galaxias swimming up small (< 20 cm) upstream obstacles into low velocity upstream reaches, and during the first round of sampling, following high rainfall, they were found in similar low-discharge intermittent streams which subsequently dried for the remainder of the study and were likely to have been previously dry. Bignose galaxias in these habitats are likely to have immigrated from surrounding populations into these temporary low-discharge habitats, suggesting that bignose galaxias may actively seek these habitats. Benefits of selecting low discharge habitats may be the lower energetic costs of foraging in slow-flowing environments (Facey and Grossman 1992), escape from interspecific competitors (Power, Matthews and Stewart 1985) or increased availability of prey in newly inundated habitats (Sommer *et al.* 2001, O'Connell 2003). In contrast to bignose galaxias biomass, the biomass of other fish increased with discharge, suggesting that other fishes benefit in these habitats which are less suitable for bignose galaxias. Mechanisms for increasing populations of other fishes with discharge may be more clear as more information exists on their habitat preferences. For example, foraging in salmonids is

dependent of invertebrate drift, which decreases with decreasing discharge, so suitability of habitats should increase for trout as discharge is related to foraging efficiency for these drift-feeding fishes lowering growth rates (Harvey, Nakamoto and White 2006) and higher discharge streams should therefore support higher salmonid biomass (Harvey, White and Nakamoto 2005, Hayes, Hughes and Kelly 2007). Habitat preference also increases with velocity for the other commonly found fishes (i.e. for alpine galaxias, koaro and Canterbury galaxias) and these fishes are likely to prefer higher discharge, high-velocity habitats (Jowett and Richardson 2008). An alternative explanation is that other species were restricted from bignose galaxias habitats by harsh physico-chemical conditions likely to exclude other fishes. However, in the spring-fed streams I surveyed temperatures remained low, which may prevent low pH and dissolved oxygen concentrations, although temperatures did approach zero in some surveyed sites which may have limited some fishes.

Discharge-based niche differences may only explain part of the relationship between bignose galaxias and other fishes, and if the niches of bignose galaxias and other fishes are not entirely separate, then antagonistic interactions, such as competition and predation, may also explain the population patterns I observed. The negative relationship between bignose galaxias and other species in this survey and their co-occurrence suggest that antagonistic interactions might influence bignose galaxias populations. Similarly, although I did not find an effect of flow on other species in my manipulation experiment, antagonistic interactions between bignose galaxias and other fishes for preferred higher-velocity habitats might still explain the low abundance of bignose galaxias in faster treatments.

A lack of detailed knowledge on the competitive ability of bignose galaxias means that outcomes of interspecific interactions for these fishes are unclear, but given they occur with fishes that commonly affect other galaxiid species, I speculate that the outcomes of any

interactions are likely to be negative. Both native koaro and introduced salmonids (brown and rainbow trout) were common in high discharge sites in this survey and both species negatively affect populations of native galaxias, especially non-migratory galaxias species, via competition and predation (Crowl, Townsend and McIntosh 1992, Allibone 1999). Furthermore, for sites where trout were present during surveys, I found strong negative trout biomass effects on total galaxias biomass. This suggests that trout-galaxiid interactions which occur elsewhere might similarly affect galaxiids in spring-fed streams. Antagonistic interactions may not be limited to competition and may also involve predation. In streams I surveyed, salmonids are the most likely predator of bignose galaxias, larger native predators, such as eels were largely absent, presumably due to downstream dams blocking migration (Jellyman and Harding 2012), and can consume all size-classes of small galaxias (McIntosh 2000). Trout larger than 150 mm were found at sites on several occasions, however bignose galaxias were able to co-occur with trout, albeit at low densities, throughout the study.

If antagonistic interactions between other fishes do influence bignose galaxias populations, then their populations may still be influenced, indirectly, by the influence of discharge on other species. Furthermore, if antagonistic interactions are important they may be a relatively recent influence on bignose galaxias. Salmonids were introduced as sport fishes following European arrival and settlement in the 1800's (McDowall 1990) and populations of koaro are likely to have increased following establishment of artificial lakes (McDowall and Allibone 1994) in the upper Waitaki, especially, Lake Benmore, established in the 1960s, which is the nearest downstream lake for both the Ahuriri River and Fork Stream. Therefore, current distributions of bignose galaxias and their restriction to low-discharge springs may differ from their historic distribution, and if antagonistic interactions are the cause, then these processes may have limited their distribution long before their discovery.

Both niche-differentiation and antagonistic interactions likely explain patterns in the populations of bignose galaxias in this study and further investigation is required to determine the contribution of each to bignose galaxias populations. Both niche-differentiation (Crow *et al.* 2010), antagonistic interactions (David and Stoffels 2003) and predation (McIntosh 2000) mechanisms are important for galaxias elsewhere and it is likely that both mechanisms influence bignose galaxias populations.

Implications

The implications of my findings for the management of bignose galaxias include consideration of the effects of discharge and antagonistic interactions with other fishes. In particular, if bignose galaxias show a preference towards stable but low-velocity, low-discharge habitats, then identifying and maintaining these habitats is likely to be important. Further investigation to determine if bignose galaxias possess physiological adaptations to occupy low-discharge habitats that are exposed to extremes of temperature and whether this limits their ability to occupy high-discharge habitats, would be especially valuable as it should help determine the likely outcomes of management efforts (i.e. control of predators and competitors) and further prioritise management efforts towards the most suitable habitats.

Low discharge habitats may also be especially vulnerable to changes in flow. With already low discharges, even minor reductions in discharge can cause these habitats to dry. This may make them especially vulnerable to climate change influences on precipitation, whether these are reductions in average precipitation or increased drought frequency (Thuiller, Lavorel and Araujo 2005). During drying, wetted areas typically contract upstream and downstream (Closs and Lake 1996, Davey and Kelly 2007). Throughout my surveys I observed similar changes in upstream wetted areas, which migrated longitudinally upstream and downstream following flooding and drought conditions. Given observations of bignose galaxias in

intermittent habitats following high flows, I suspect that these fishes move longitudinally along streams tracking upstream low-discharge wetted areas. Changes in precipitation which expand or contract the range of wetted areas, may restrict fish to areas below critical habitats. For example, under increasingly prolonged drought conditions, springheads may completely dry and forcing bignose galaxias populations into downstream main stem habitats where antagonistic interactions become more severe. Alternatively, under increased precipitation causes increases in and discharge,, populations of other fishes may benefit, increasing antagonistic interactions for bignose galaxias and negatively affecting their populations.

The degree to which habitats were used by bignose galaxias varied along a discharge gradient across sites, and the range of bignose galaxias biomass observed likely reflected a gradient of habitat suitability and productivity. Therefore, habitats are likely to fulfil differing roles for bignose galaxias populations, dependent on discharge, and collectively may form meta-populations (Falke and Fausch 2010). Such meta-populations have been investigated for galaxiids. For example, source populations above barriers to trout-migration were important for the persistence of Canterbury galaxias in trout-invaded reaches (Woodford and McIntosh 2010). If bignose galaxias populations form part of larger meta-populations, then identifying and maintaining access to these habitats will require protection of these habitats and maintaining connectivity between populations, both of which are likely to be discharge-dependent.

Conclusions

I found that populations of a threatened fish limited to springs were influenced by local habitat conditions and by populations of other fishes. It appears likely that both influences interact, and that these interactions are mediated by discharge. Understanding this interplay between abiotic and biotic interactions may be especially important for managing populations

of habitat specialist species in response to changes in the environmental conditions which maintain their habitats.

Tables and Figures

Table 1. Summary of mean habitat conditions and species found at survey sites. Abbreviations for fish biomass is as follows: (galbre) koaro (*Galaxias brevipinnis*); (galmar) bignose galaxias (*Galaxias macronasus*); (galpau) alpine galaxias (*Galaxias paucispondylus*); (galpro) upland longjaw galaxias (*Galaxias prognathus*); (galvul) Canterbury galaxias (*Galaxias vulgaris*); (gobbre) upland bully (*Gobiomorphus breviceps*) ; (oncmyk) rainbow trout (*Oncorhynchus mykiss*); (saltru) brown trout (*Salmo trutta*). Ahuriri-1 (us) and (ds) represent upstream and downstream respectively, the downstream site was established after the upstream site dried. Sampling occasions are only included for wetted conditions.

				Fish biomass (g/m^2)							
Site name	Sampling occasions	Width (m)	Discharge (m^3/s)	galbre	galmar	galpau	galpro	galvul	gobbre	oncmyk	saltru
Ahuriri-1 (us)	2	0.9	0.029	0.16	1.51	0.73	-	-	0.05	-	0.56
Ahuriri-1 (ds)	4	1.3	0.012	-	1.22	0.39	-	0.36	-	-	-
Ahuriri-2	5	0.8	0.002	-	3.30	-	-	0.24	-	-	-
Ahuriri-3	1	0.7	0.002	-	3.87	-	-	-	-	-	-
Ahuriri-4	4	1.0	0.006	-	1.22	-	-	-	-	-	0.05
Ahuriri-5	5	2.0	0.037	-	0.84	0.01	-	0.06	-	-	2.50
Fork-1	6	1.8	0.057	-	0.58	0.09	-	-	-	0.19	6.13
Fork-2	6	2.6	0.042	-	3.05	0.01	0.09	0.06	-	0.04	1.04
Fork-3	6	1.7	0.040	0.11	0.15	1.34	-	0.42	-	0.15	1.09
Fork-4	6	1.6	0.043	0.88	0.32	0.12	-	0.05	-	1.71	0.13
Fork-10	5	2.4	0.104	< 0.01	0.39	2.22	0.02	0.54	-	-	-

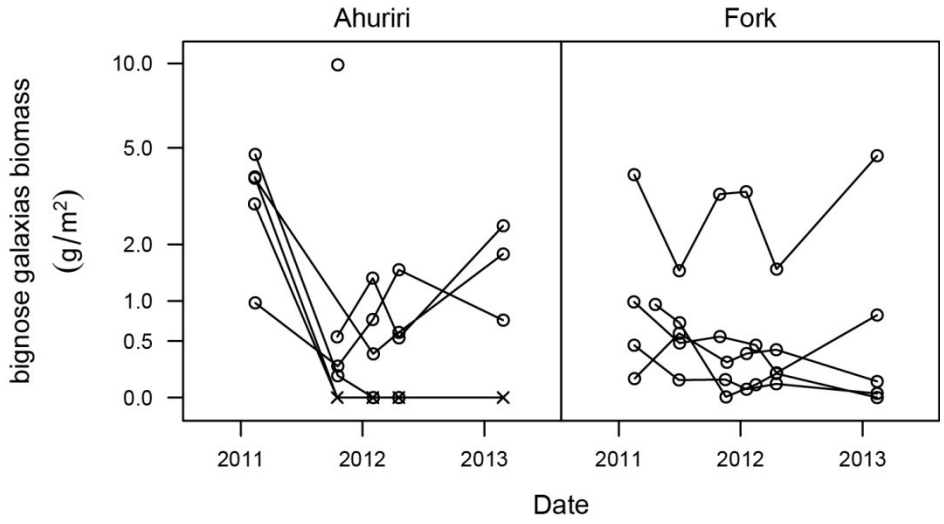

Figure 1. Seasonal changes in bignose galaxias biomass over the survey period. Circles represent visits where streams were wetted and plus symbols show a site was dry during visit. Ahuriri sites were unable to be accessed during June 2011 period due to weather.

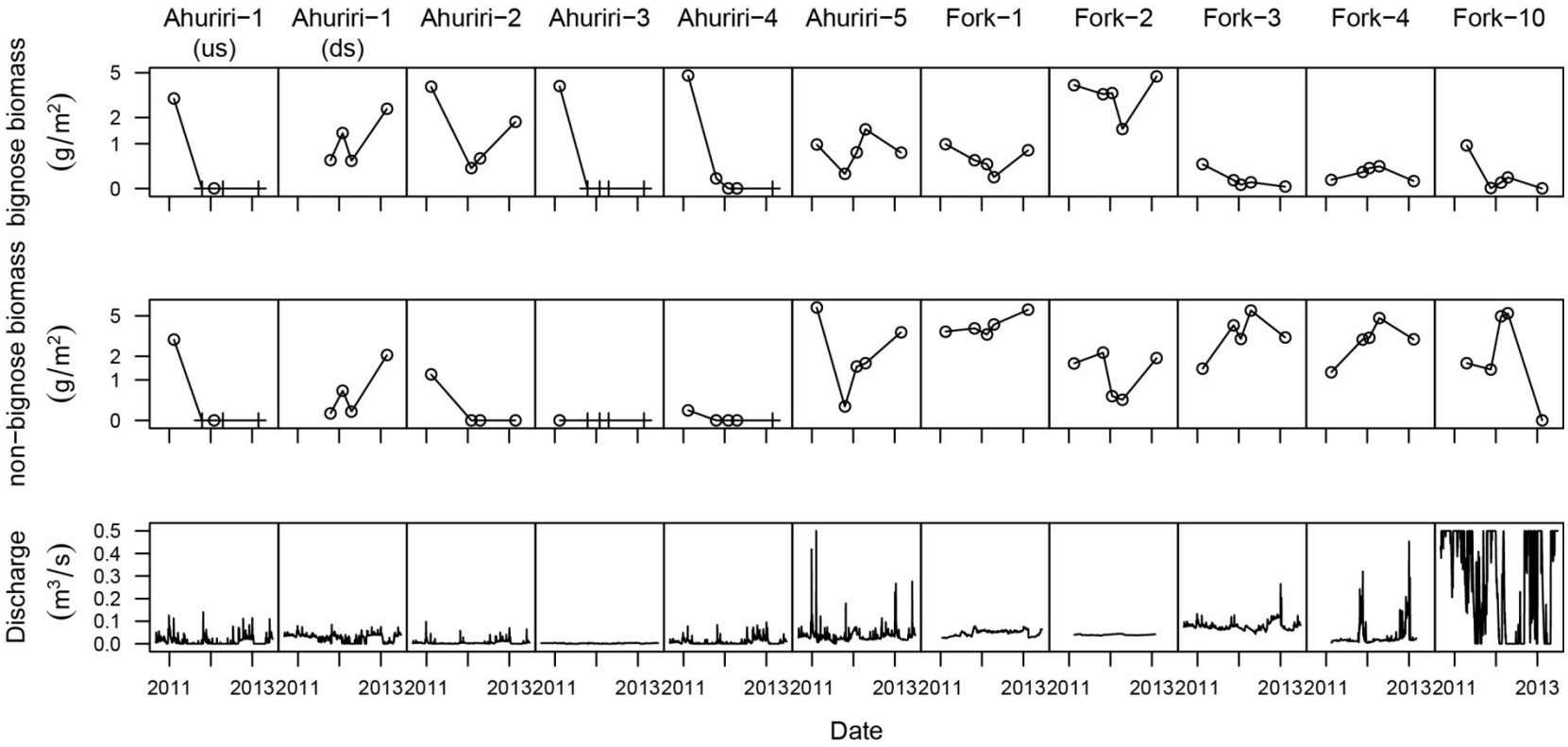

Figure 2. Changes in fish biomass and discharge over time at all sites in the survey. Fish biomasses are shown on a log-scale and circles represent visits where streams were wetted and plus symbols show a site was dry during visit. The discharge axis is clipped to 0.5 m^3/s to allow the display of other sites.

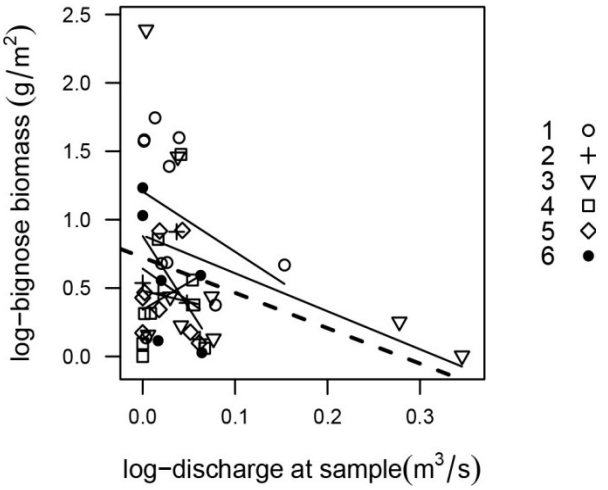

Figure 3. Changes in bignose galaxias biomass across a gradient of discharge for each sample period. Each line represents a linear relationship between log-transformed bignose galaxias biomass and discharge across all sites for replicate samples taken over time and symbols represent sampling periods. The dashed line represents the fitted effect of discharge across all time periods as fitted using a random-intercept linear mixed model.

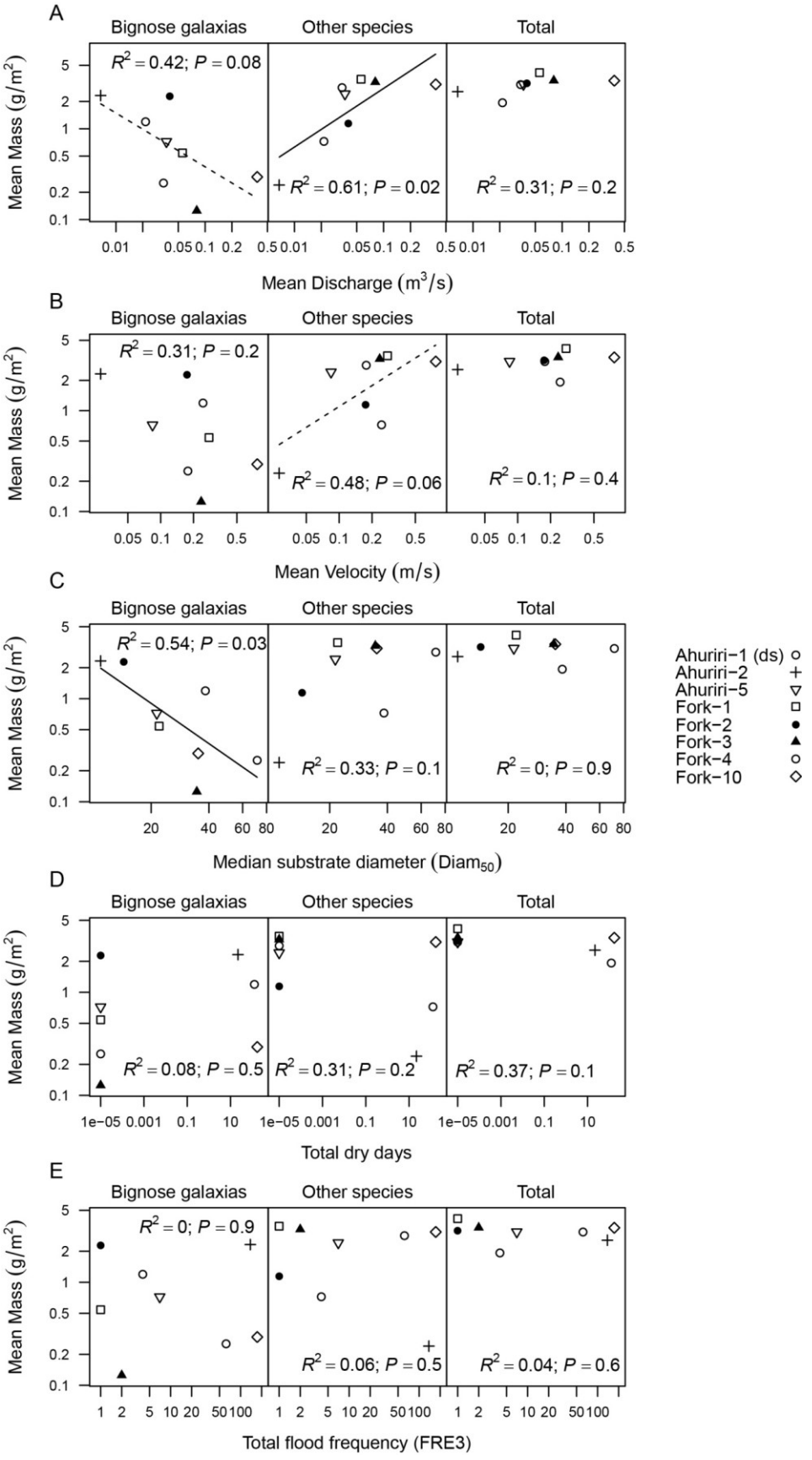
A
Bignose galaxias
Other species
Total
$R^2 = 0.42$; $P = 0.08$
$R^2 = 0.61$; $P = 0.02$
$R^2 = 0.31$; $P = 0.2$
Mean Mass (g/m^2)
Mean Discharge (m^3/s)
B
$R^2 = 0.31$; $P = 0.2$
$R^2 = 0.48$; $P = 0.06$
$R^2 = 0.1$; $P = 0.4$
Mean Velocity (m/s)
C
$R^2 = 0.54$; $P = 0.03$
$R^2 = 0.33$; $P = 0.1$
$R^2 = 0$; $P = 0.9$
Median substrate diameter (Diam$_{50}$)
Ahuriri−1 (ds)
Ahuriri−2
Ahuriri−5
Fork−1
Fork−2
Fork−3
Fork−4
Fork−10
D
$R^2 = 0.08$; $P = 0.5$
$R^2 = 0.31$; $P = 0.2$
$R^2 = 0.37$; $P = 0.1$
Total dry days
E
$R^2 = 0$; $P = 0.9$
$R^2 = 0.06$; $P = 0.5$
$R^2 = 0.04$; $P = 0.6$
Total flood frequency (FRE3)

Figure 4. Changes in mean biomass of bignose galaxias and other fishes with flow and physical conditions. Relationship between bignose galaxias and non-bignose galaxias biomass and (A) mean discharge, (B) mean velocity, (C) mean median substrate diameter, (D) total dry days and (E) total frequency of flows greater than three times the median flow (FRE3). Biomasses shown are site means across all samples over time for each site and are only shown for sites with greater than three samples over time. Discharge and velocity are means, and total dry days and flood frequency are totals, taken from discharge estimates over the entire study period. Median substrate diameter is a mean from all samples over time.

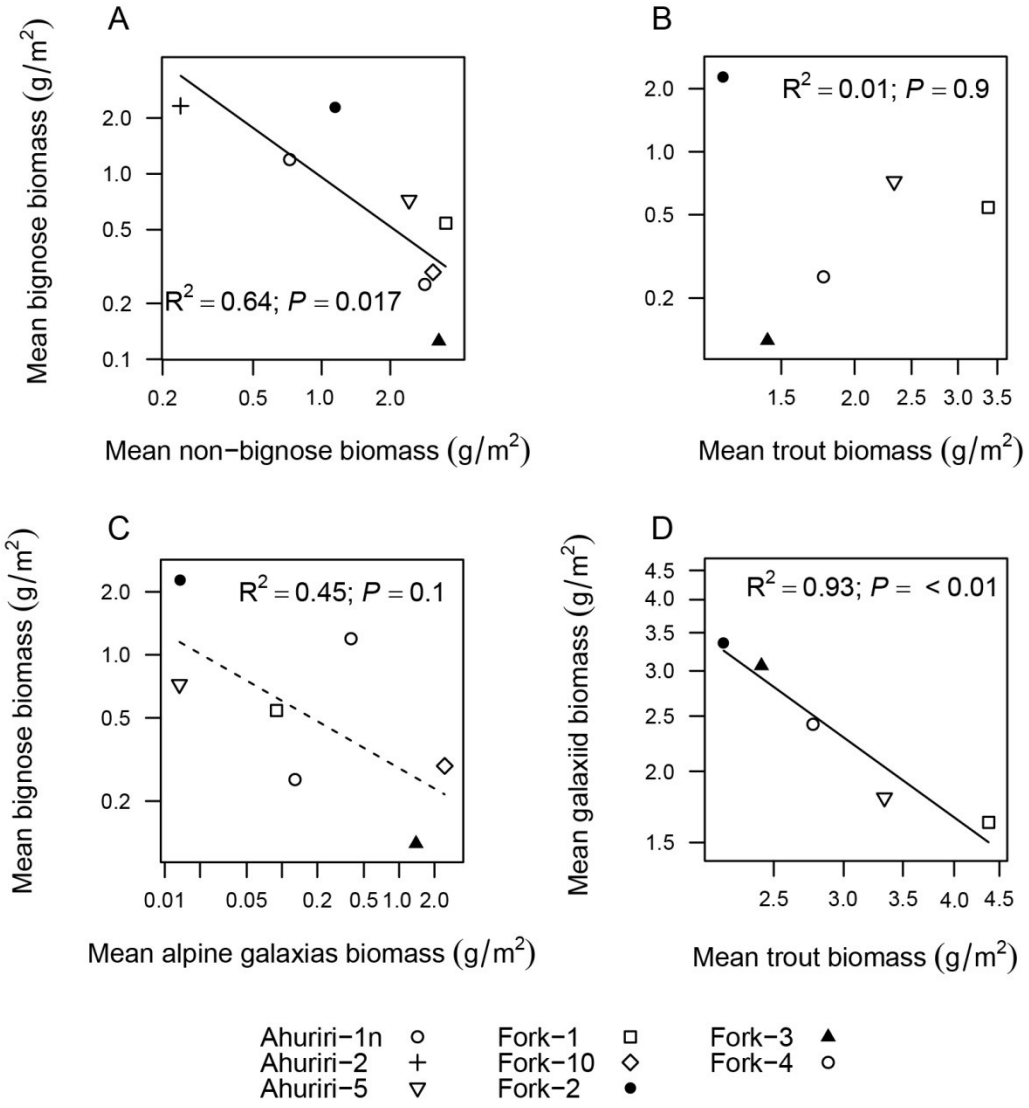

Figure 5. Biomass of bignose galaxias and likely antagonistic species: (A) non-bignose galaxias biomass, (B) total trout biomass and (C) alpine galaxias biomass, and (D) the relationship between total galaxiid biomass and total trout biomass. All biomasses are shown on a log-scale and regressions are based on log-transformed values. Points for sites where antagonistic species were absent for the entire study are omitted.

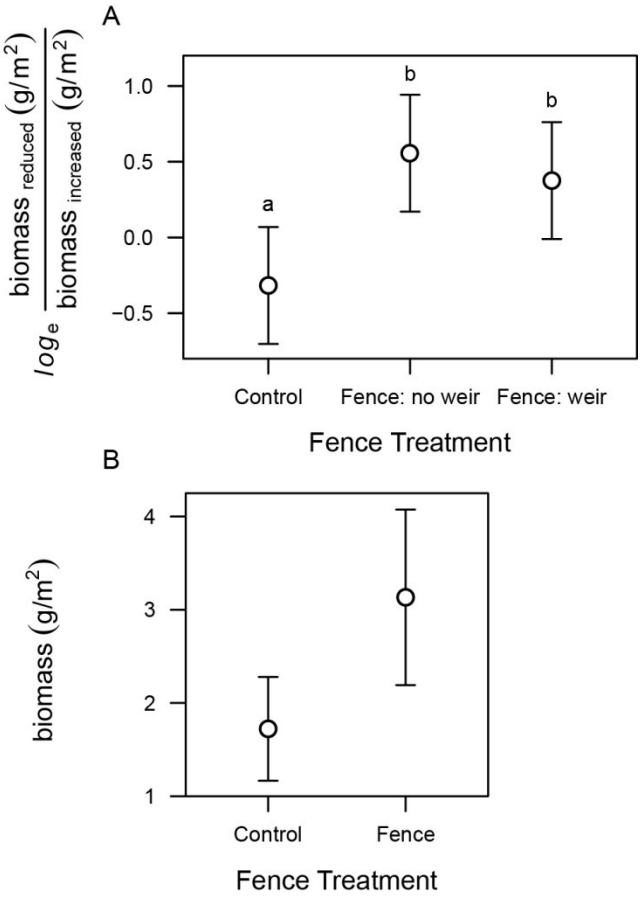

Figure 6. Mean difference in biomass between high and low discharge treatments within fenced sections of stream. Response values represent the log-ratio of the biomass (g/m^2) from low discharge treatments divided by high discharge treatments. Error bars represent 95 % confidence intervals of fitted means.

Plate 6. A hillslope-fed spring where bignose galaxias (*Galaxias macronasus*) are usually found.

Chapter Five:

General Discussion

In this chapter I incorporate findings from previous chapters into a general framework for approaching the conservation of threatened fish confronted with global change, and how characteristics of stream ecosystems may influence the importance of these drivers. The overall aim of this thesis was to investigate how populations of threatened fishes, bignose galaxias (*Galaxias macronasus*) and upland longjaw galaxias (*Galaxias prognathus*), responded to current changes and patterns in their environment, to inform how global changes are likely to affect their populations.

In Chapter Two this involved determining how multi-scale flow-related drivers influenced fish populations and communities across regulated and unregulated sub-catchments and reach-, meso- and micro-scale habitats. Chapter Three examined how populations of a threatened fish in disturbed braided rivers, upland longjaw galaxias (ULG), responded to large flow disturbances, and how this influenced habitat availability and use in these rivers. Finally, in Chapter Four I investigated how flow -influenced populations of a spring-head habitat specialist fish, bignose galaxias, and populations of other fishes across a discharge and disturbance gradient. Generally, each chapter examined progressively more local-scale drivers of populations of each of the threatened species, but because stream ecosystems are strongly hierarchical and unidirectional, these local-scale drivers are also dependent on larger scale processes. Therefore, the processes which drive populations of these threatened fishes are likely vulnerable to changes associated with global change drivers, acting across multiple scales. To fully understand the potential impacts of global changes on threatened fishes, we need to view those processes which drive their populations within a framework which

incorporates the spatially constrained, multi-scale and hierarchical nature of stream ecosystems (Frissell *et al.* 1986, Jackson, Peres-Neto and Olden 2001), as well as the large influence of flow regime (Poff *et al.* 1997).

In Chapter One I summarised those global change drivers likely to threaten freshwater ecosystems and highlighted those which were most likely to affect fish communities in the upper Waitaki River, where the two threatened galaxiids occur. Specifically, those drivers were flow modification, habitat degradation and destruction, and species invasions. Flow-related influences on fish populations and communities were found across all of the chapters and suggest that global -change drivers have either, likely already affected, or have the potential to affect, fish populations in the upper Waitaki River. In this Chapter, I summarise the current, and potential, effects of flow modification, habitat degradation and destruction, and species invasions on the threatened fishes I studied.

Influence of global changes on upper Waitaki River threatened galaxiids

Among the potential global changes, flow modification is especially damaging to stream ecosystems because it alters processes which maintain and structure aquatic habitats (Brandt 2000, Petts and Gurnell 2005, Poff *et al.* 2007). The strong contemporary and potential influence of flow modification was a common theme across all chapters. In Chapter Two, flow modification strongly influenced the distribution of fishes, and altered the composition of fish communities in regulated sub-catchments. Flow regulation was included in the best models which explained species occurrences for all species it could be tested for, and also drove large changes in community composition as well as changing the composition of habitats downstream of regulated rivers. These differences are most likely due to a reduction in flow-related disturbances in regulated rivers, favouring species which were competitively-dominant over those species which were disturbance-tolerant.

The direct effect of flow modification on upland longjaw galaxias (ULG) and bignose galaxias were unable to be examined because these fishes were only found upstream of regulated sub-catchments during surveys, and in other surveys were also seldom found in, or below, regulated rivers. This distribution potentially reflects the past effects of flow regulation, which took place before their discovery. However, populations of both ULG and bignose galaxias were influenced by contemporary flow-related processes which would likely be influenced by any future flow modification. Therefore, flow modification has a large potential future influence on upland longjaw galaxias (ULG) and bignose galaxias. For example, large and frequent disturbances were likely responsible for the low densities of competitors in ULG habitats, reducing habitat competition in the braided rivers where they occurred. Therefore, flow modifications which lower the magnitude and frequency of disturbances would likely have a negative influence on ULG populations via increases in populations of other fishes, increasing competitive interactions and reducing ULG populations.

For bignose galaxias, mean flow conditions influenced their populations and populations of other fishes in spring-fed habitats. Bignose galaxias populations were largest in habitats within a narrow window of very low flows, while the abundance of other fishes increased with increasing flow (Chapter 2). This pattern meant that flows also influenced the potential for interspecific interactions between bignose galaxias and other fishes, and therefore changes to flows may intensify or reduce harmful species interactions between bignose galaxias and other fishes. Flow modification currently has a large influence on fish populations and communities in the regulated upper Waitaki River catchment and most likely promotes the persistence of introduced salmonids in regulated rivers, where they would otherwise be removed by large disturbances.

Aside from the likely degradation of fish habitats that had already occurred prior to their discovery and concern for these native fishes, I did not detect any effects of habitat degradation on populations of bignose galaxias and upland longjaw galaxias. However, my surveys were designed to investigate the influences of flow on these fishes, not habitat degradation, so were not conducted over a gradient of habitat degradation. However, there is likely still a high potential for the habitats of these threatened galaxiids to be degraded or destroyed. These potential threats are indirect, via changes that alter the processes which currently maintain their habitats, and direct via local habitat degradation.

In particular, any changes to flow regimes are likely to alter the processes which maintain habitats for these fishes, indirectly affecting their populations. For bignose galaxias, because their habitats are largely spring- or wetland-fed, changes to the underlying hydrology via large-scale changes in precipitation, or changes in flows in adjacent large rivers, are likely to influence flow in springs (Ward *et al.* 2002). Moreover, because their habitats are very low discharge, even small changes in flow may cause their habitats to dry, effectively degrading or destroying habitats, meaning the suitability of their habitats is dependent on a very narrow range of discharge. Similarly, habitats for ULG habitats were likely maintained by shifting substrates and sediment transport during high disturbances. The braided rivers I surveyed also had a large amount of shallow and slow habitats, likely due to their braided character (Mosley 1982). These slow and shallow habitats were used by ULG so changes which alter braiding in these rivers would affect ULG by altering the abundance of these habitats.

Bignose galaxias are most likely to be especially vulnerable to the direct effects of localised habitat degradation because their populations are locally abundant in very small reaches. This is best illustrated by the circumstances which led to their discovery. Following likely degradation of their habitat by partially draining a wetland for irrigation, they were

discovered during a *post-hoc* faunal survey for a water consent (McDowall and Waters 2003). Other local-scale changes likely leading to habitat degradation for bignose galaxias include damage to stream banks and in-stream habitat by stock intrusion, drainage or changes to their habitats for agriculture and irrigation, and changes in sediment input associated land use changes. Conversely, ULG may be less vulnerable to localised habitat degradation because their habitats are distributed across large riverbeds, and are regularly destroyed and replaced by large disturbances. Although, if very localised habitats play an important role for ULG population persistence, then degradation to these habitats may make them vulnerable to habitat degradation (Figure 1B). Because habitat degradation can have direct and indirect causes which vary the spatial extent of their impacts, the vulnerability of these threatened fishes to potential habitat degradation relates to the spatial scale at which habitat degradation occurs, as well as the spatial extent of their populations.

Populations of invasive species were likely an important influence for both threatened fishes. Introduced salmonids were common throughout the region where both fishes occur (Chapter Two). Because both native fishes have only been recently discovered and are under-studied, the historical effects of salmonid introduction for these threatened galaxiids are largely unquantified. However, the effects of introduced salmonids on other non-migratory galaxiids suggests that any effects might be expected to be negative. In Chapter Two, invasive species dominated regulated river fish communities, and overall, native fish were more abundant in unregulated rivers. These effects couldn't be tested for bignose galaxias, or ULG, because they were not found in regulated rivers, but their interaction with introduced salmonids likely played a role in their absence from the regulated rivers. In Chapters Three and Four, both ULG and bignose galaxias were mainly found where densities of other fishes were low and

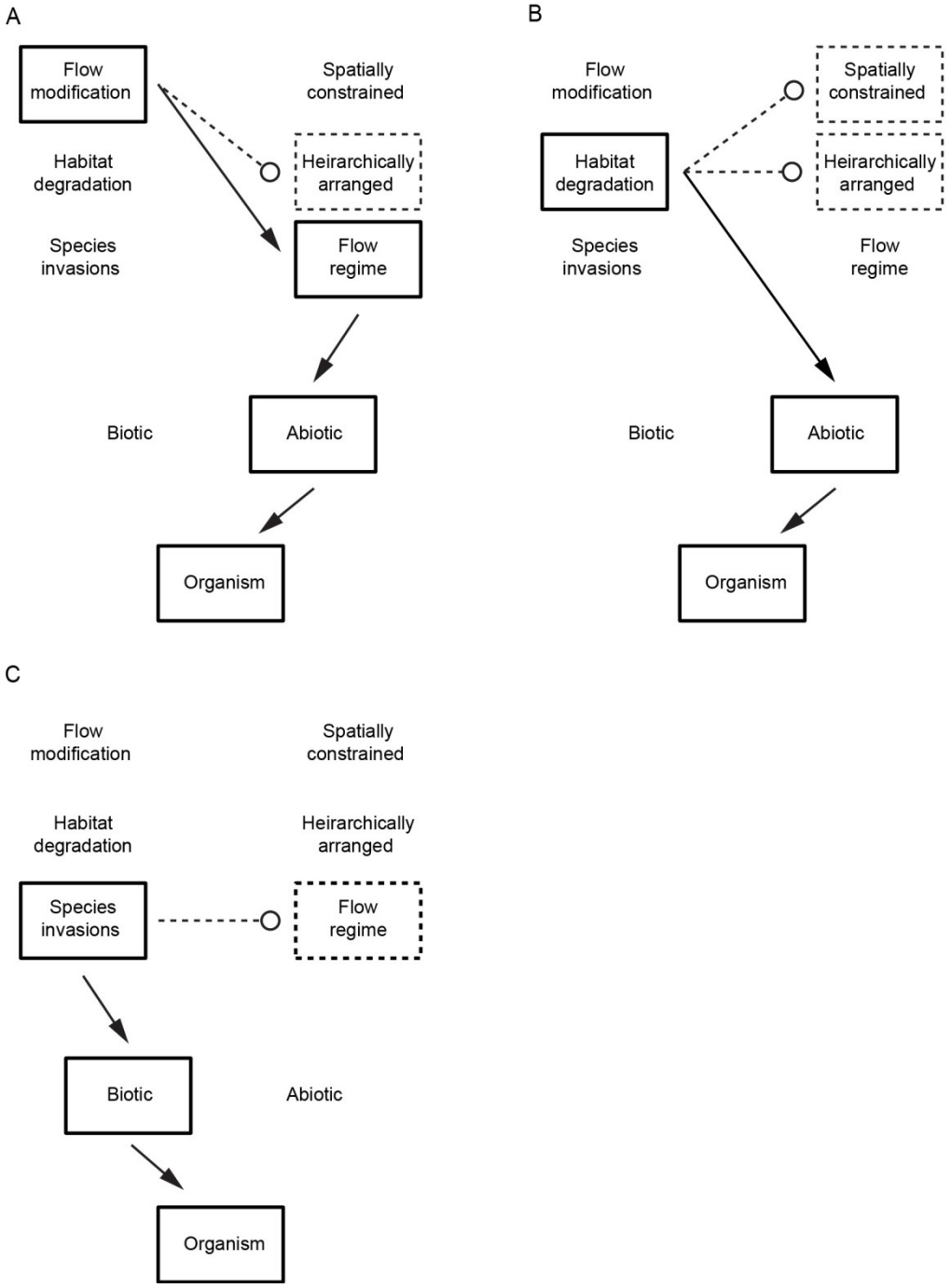

Figure 1. The influence of flow modification (A), habitat degradation (B) and species invasions (C) relevant to stream fish on abiotic and biotic habitat filters, and the influence of stream ecosystem characteristics on these global change drivers. Solid arrows and boxes indicate direct effects, dashed lines with circle bases and boxes represent the influence of stream characteristics on global changes.

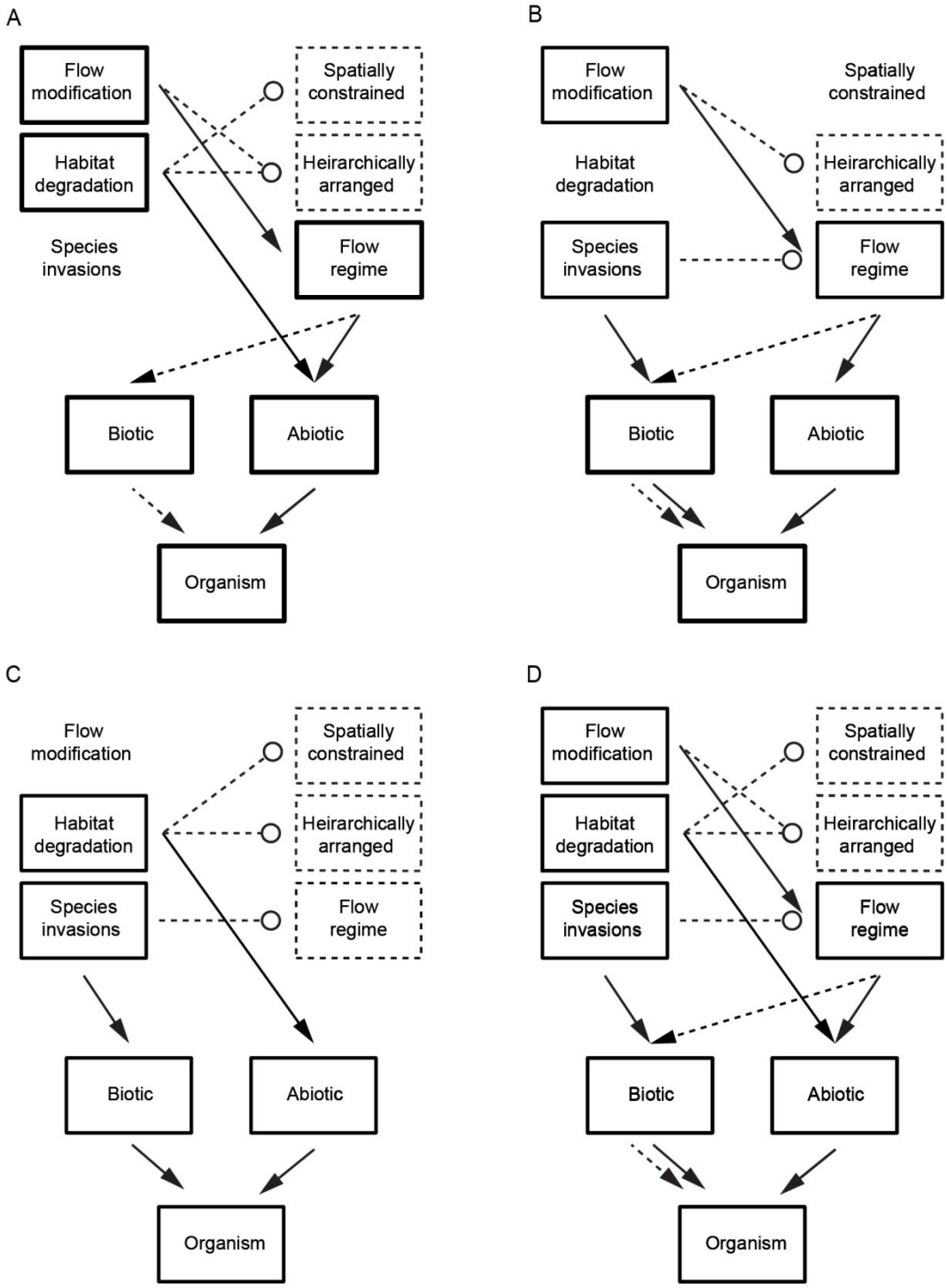

Figure 2. The interacting influence of; flow modification and habitat degradation (A); flow modification and species invasions (B); habitat degradation and species invasions (C) and the effects of all three global change drivers (D), relevant to stream fish on abiotic and biotic habitat filters, and the influence of stream ecosystem characteristics on these global change drivers. Solid arrows and boxes indicate direct effects, dashed lines with circle bases and boxes represent the influence of stream characteristics on global changes.

this probably reflects a low competitive ability in the presence of other fishes. This poor competitive ability means these fishes are likely indirectly influenced by factors which affect populations of their competitors.

Overall, interactions between global change drivers are likely to be more common in stream ecosystems because streams are highly connected across scales, linking these drivers, making stream ecosystems especially susceptible to global changes. For example, flow modification may also degrade habitats via changes to the flow regime, which drives processes that create habitat (Figure 1A; Figure 2A). Similarly, flow modification, via its influence on flow regimes, can influence outcomes of species invasions, determining the potential for harmful biotic interactions with receiving fish communities (Figure 2B). Additional combinations of interactions between global change drivers exist and are discussed below along with specific recommendations and considerations for bignose galaxias and ULG in the upper Waitaki River.

Overall, the structure of streams, specifically that they are spatially constrained, hierarchically arranged and strongly linked to flow regime, means that alterations to flow and the presence of invasive species may have a greater influence on species like bignose and ULG.

Management recommendations

Flow modification has a large influence on the flow regime of rivers (Figure 1A) and this can favour populations of invasive species (Figure 2B; Gido and Brown 1999, Marchetti *et al.* 2004). Consequently, this can potentially disrupt processes that create habitats, leading to habitat degradation (Figure 2A), so flow modification is likely to have a large influence on populations of bignose galaxias and ULG. For ULG, specific consideration should be given to how flow modification is likely to alter the distribution of their habitat. The shallow and

slow habitats they occupy are likely associated with braiding in these rivers. Under modified flows a loss of braiding is common because the channel becomes less mobile due to changes in stream power and unchecked vegetation growth, which stabilises channels (Brandt 2000, Petts and Gurnell 2005). The springs that bignose galaxias occupy are maintained by hydrological connections with surrounding water bodies (Ward *et al.* 2002). Modifications to flows in the surrounding landscape, especially in adjacent wetlands and main stems of rivers, may affect flows in springs. Because of the small ranges of flows bignose occupy, even small hydrological changes have the potential to eliminate their current habitats. Furthermore, for both fishes, the importance of meta-populations is unknown, so it may also be important to protect multiple populations of fishes, especially for bignose galaxias where entire reaches containing populations may dry (Chapter Three). Therefore, to maintain habitats for these fish, flows and hydrological connectivity in surrounding habitats need to be protected as well as those flows in their immediate habitats. Refugia and other peripheral habitats may also be important, meaning sufficient flows are needed between habitats to maintain surrounding habitats and to maintain connectivity between these habitats.

Both bignose and upland longjaw galaxias occur at contrasting habitat extremes, in highly stable and disturbed habitats, respectively. For bignose galaxias, this means very local habitat conditions are particularly important while for upland longjaw galaxias whole river dynamics are especially important.

Protecting ULG habitats from degradation is likely made more difficult by the distribution of their habitats across large braided rivers and the constant removal and creation of their habitats. This large spatial extent and frequent re-assortment probably protects their populations from localised habitat degradation, but because the processes which likely maintain their habitats are complex and hierarchically controlled by very large scale

processes, they are likely most vulnerable to habitat degradation which occurs due to changes to the overall flow regimes of braided rivers (Figure 2B; Brandt 2000, Petts and Gurnell 2005). However, the degree to which ULG potentially use more permanent and discrete habitats is largely unknown. Such habitats would likely be much more vulnerable to localised habitat degradation than the braided river habitats. If discrete stable side channels or the like are shown to be important for maintaining ULG populations, potentially providing spawning or refugia habitat, then their protection will be critical to maintaining ULG populations.

Bignose galaxias were largely restricted to spatially confined reaches at the upstream extremes within larger stream networks, making them especially vulnerable to localised habitat degradation. Any degradation to these habitats would affect the large proportions of their population and the relative isolation of these habitats. Fortunately, this localised distribution may also make their habitats suitable for more active management measures which would be less viable across larger areas. For example, fencing to prevent stock intrusion might be more feasible because fenced areas would be relatively small in extent. Likewise, identifying the hydrological mechanisms which underpin flows in these headwater springs is likely to be more feasible.

Introduced salmonids were the primary invasive species that occurred with ULG and bignose galaxias. Populations of trout appear to benefit from flow modification, presumably by reducing or eliminating the effects of large disturbances. Therefore, the potential impact of salmonids on the threatened galaxiids is also dependent on the effects of flow modification via its effect on prevailing flow regime (Figure 1B, Figure 2B). Currently, frequent flow disturbances appear to limit populations of most other fishes in rivers where ULG were found. Therefore the impacts of introduced salmonids might be expected to be low. However, the potential for negative interactions between ULG and salmonids may occur in more

discrete stable side streams which ULG may use only occasionally. Furthermore, salmonids are also likely to impact ULG if flow regime changes, reducing the frequency and magnitude of disturbances which currently make the rivers ULG occupy unsuitable for salmonids.

Bignose galaxias often co-occurred with salmonids, and it is possible that salmonids are food-limited in the low-velocity upstream habitats bignose galaxias commonly occupied. However, bignose galaxias populations were lowest in streams with high abundance of potential competitors, suggesting they are poor competitors, and the restriction of bignose galaxias to upstream habitats might be the result of competitive and predatory interactions. The majority of bignose galaxias populations surveyed for this thesis had co-occurring populations with salmonids and actively preventing contact between salmonids and bignose galaxias is likely to be challenging. However, because bignose galaxias populations were so spatially constrained, this increases the viability of more active measures to control salmonids in bignose galaxias habitats. Weir construction to prevent salmonids access is an active measure capable of limiting the spread of salmonids. However, if salmonids are already present prior to weir installation then salmonids may also need to be removed. Salmonid removal can be prohibitively costly or challenging over large areas, so focusing efforts on populations which are limited to smaller areas may increase the efficacy of removal. Such active approaches should also consider the proximity of salmonids colonists as a likely re-invasion source and focus management on populations which are further from downstream lakes and regulated rivers where salmonid abundances are higher.

Management of ULG and bignose galaxias is likely to be especially difficult because many of the changes which influence their populations are already well-established and are likely to interact (Figure 2D), making management outcomes dependent on multi-scale processes which act from catchment to micro-habitat scales.

While threats to galaxiids in the upper Waitaki River act across multiple scales making their management particularly challenging, specific knowledge of factors that influence their distribution and population persistence should greatly aid conservation efforts by recognising the scale at which threats to populations operate. Conservation efforts for these threatened fishes can be prioritised to target those threats which occur over smaller scales and also avoid areas where larger scale threats are likely to over-ride the success of local-scale management.

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